LATVIJAS UNIVERSITĀTE

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Latvijas rāpuļu ekoloģija: vides faktoru saistība ar sauszemes rāpuļu izplatību un skaitu

Ecology of Latvian reptiles: environmental factors and abundances of terrestrial reptiles

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CONTENTS

1. INTRODUCTION

Numerous factors can affect the distribution and abundance of reptiles, such as climate, topography, habitats, and various anthropogenic impacts. The influence of some of these factors is relatively well studied, while the connection with others has possessed less attention from scientists. Thus, the importance of local climate is largely overlooked in the lowland temperate-zone Europe, where its effect is far less obvious than in the mountain ranges or at the species latitude distribution limits (Gaston 2003). Habitats of European reptiles have been described in detail at least for some species (e.g. Stumpel 1985, 1988, Strijbosch 1988, Glandt 1991), although this information (especially from warmer climate zones) is not always applicable to Latvia. The number of studies in temperate Europe on reptile ecology is still insufficient due to their low overall density and very uneven distribution. Most of the studies are limited to only a few sites, and (or) only to 1-2 species in each case (see Introduction in Chapter 4). The understanding which climate and habitat characteristics are important for reptile abundance is especially valuable in reptile conservation efforts such as the establishing and management of protected areas.

Although the first information about reptiles in the territory of modern-day Latvia was published by German authors already in 18th and 19th centuries (e.g. Fischer 1791, Drumpelman & Friebe 1806), data on species ecology in Latvia is still scanty. Probably still the most comprehensive information about reptiles in Latvia was published before World War II in a popular booklet (Siliņš, Lamsters 1934). The latter data are either also the publications in popular journals or books (e.g. Spuris *et al.* 1974) or the annotated species lists for particular areas (e.g. Barševskis *et al.* 2002).

The aim of the present study was to find out environmental factors that determine spatial distribution and abundances of native lizard and spake species, from large-scale (such as climate and broad habitat groups) to small-scale factors (such as vegetation composition and structure). The specific tasks of the work were the following:

- To collect the reptile abundance data representative for all the territory of Latvia;

- To find out relationships between reptile abundances and specific climate factors and habitats;
- To describe the composition and structure of vegetation on reptile sites and to clarify important vegetation factors;
- To study the relative abundances of reptiles in forest habitats, and to clarify forest type and forest stand preferences;
- To verify distribution data of a rare species – the Smooth Snake (*Coronella austriaca*), to provide description of its habitats, and to evaluate the status of the currently known populations.

The thesis consists from the introduction part, the four chapters each written as separate survey with own introduction, methods, results and discussion parts, and the main conclusions. Chapters 2 and 4 are manuscripts in press and submitted respectively; Chapter 3 is rewritten from two publications (Čeirāns 2002*a*, 2004), and Chapter 5 – based on a separate publication (Čeirāns 2000).

2. EFFECT OF REGIONAL CLIMATE AND HABITAT TYPE ON REPTILES IN LATVIA

2.1.Introduction

Numerous factors can affect the distribution and abundance of reptiles, including climate, topography, habitat composition, and intensity of various anthropogenic impacts. Many studies have been done on habitats of European reptiles (e.g. House & Spellerberg 1983, Stumpel 1985, Berglind 2000), but the role of climate factors in temperate-zone Europe has been largely overlooked. The influence of climatic factors is perhaps best tested at species' distribution limits, either latitudal or altitudinal (Gaston 2003). The significance of climatic factors in influencing the occurrence of reptiles in lowland temperate-zone Europe, where many species have large ranges, remains obscure. Reptiles are ectotherms, and their ecology and habitat preferences can be strongly determined by regional climate (Jablokov 1976, Pikulik *et al.* 1988). Thus, knowledge of preferred climatic conditions also is important for species conservation, particularly establishment of protected areas. Latvia is a relatively small lowland country. Nevertheless, it has a marked climate transition from relatively maritime in the west to more continental in the east (Kavacs 1995), making it very suitable for climate-related research.

Recent practice in climate and landscape studies of reptiles is to use GIS with base layers of data on climate, land cover, topography, and presence-absence of species (Guisan & Hofer 2003, Raxworthy *et al.* 2003). In contrast, the present study is based on extensive fieldwork and uses multiple regression to predict relative species abundance from climatic and habitat variables. Such approach would be more sensitive than the usage of only presence-absence data.

This study presents some of the results of a wider survey (see also Chapter 4) conducted to clarify the factors determining distribution and abundance of reptiles in Latvia. Here, I consider only the influence of climatic and habitat factors. Habitats are regarded in very broad sense, e.g. forest habitats include not only more or less closed forest, but various ecotopes (clearings, cuttings etc.) as well. The average human population density on each study plot also was selected for analysis, as an indicator of the impact of potential settlement and direct human presence (killing of snakes etc.). Information from topographic maps about altitude and the surrounding landscape (forest, open landscape, mire, urban area) also was used.

Because reptile abundance also is affected by local factors, I included variables characterizing the various transects (e.g. proportion of different verge types) in my original analyses. However, as none of these factors were significant, I left them out of the analyses printed here.

2.2. Methods

2.2.1. Study area

Latvia is located on the Mid-Eastern coast of the Baltic Sea, from 55-58 ° latitude and 21-28 ° longitude. About 60 % of the territory lies below 100 m a.s.l., and only 3 % above 200 m (Kavacs 1997). Average temperatures range from –3 to –7 °C in January, and 16.5 – 17 °C in July, average annual precipitation is 550-850 mm, sum of active temperatures 1770-2155 °C (Kavacs 1995). The entire country is in the sub-boreal forest zone and about 45 % of it is covered by forest, dominated by Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* L.), and birch (*Betula pendula* Roth, *B. pubescens* Ehrh.) (Broks 2003); about 5 % of the country consists of mires, mostly of the raised-bog type (Kavacs 1997). Large-scale anthropogenic impact in Latvia is moderate: population density in Latvia is low, less than 15 inhabitants per km^2 (Overview of the Latvian indicators of sustainable development, 2003), and management of agricultural lands was mainly of low intensity during the study time (Bergkaute *et al.* 1999).

2.2.2. Sampling

Sampled sites were selected at random from stratified plots. Twenty 25x25 km plots from the Baltic Coordinate System were chosen, 1-5 in each geo-botanical region of Latvia. Geo-botanical zoning was employed because it encompasses many factors, such as soil, geology, geomorphology, and climate, not just vegetation characteristics

(Kavacs, 1995). Three to five 5x5 km squares were randomly selected from each 25x25 km plot (total of 92). The number of selected squares in each region was roughly correlated with its area (Fig. 1). Reptiles were counted on transects that crossed 5x5 km squares through their central parts using the road, path and forest cutting networks.

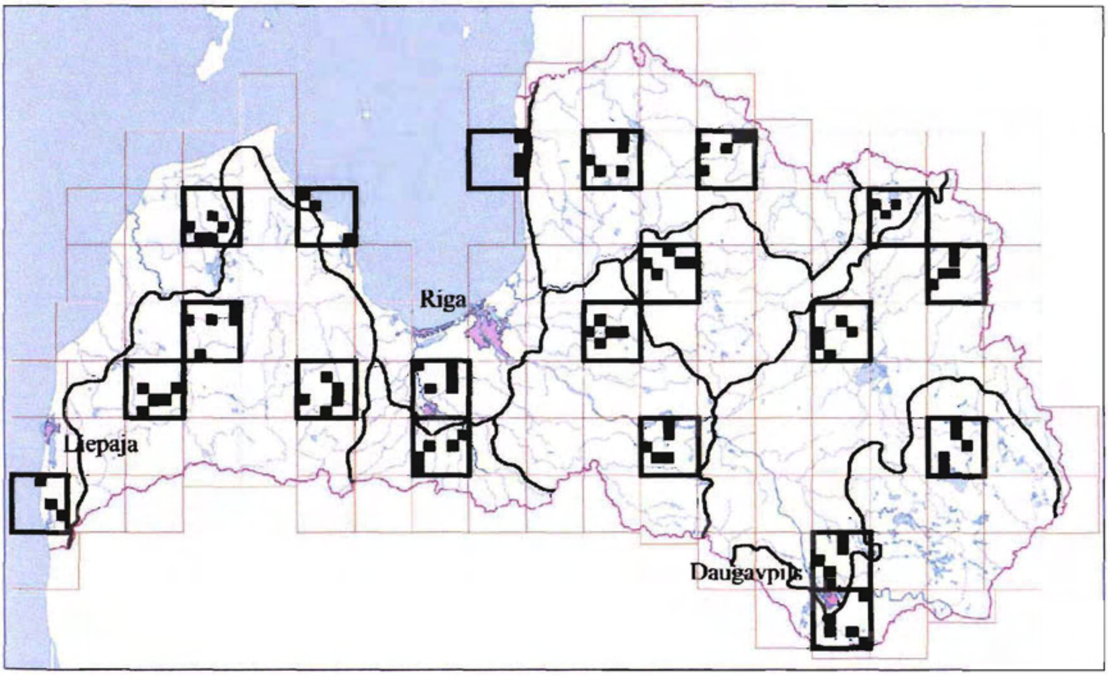


Figure 1

Location of sampled 25x25 km plots and sampled 5x5 km squares in geobotanical regions of Latvia

Censuses were carried out mostly along verges of minor roads and paths to facilitate walking and observation of reptiles. Censuses were carried out once on each transect, in the field seasons (May-September) of 1999-2003. As the activity and observed frequency of reptiles vary during a season (e.g. Jablokov 1976, Kosov 1983, Glandt 1995), transects in the same 25 km plot were surveyed in different months to reduce the impact of this factor on abundance estimates. Similarly, transects within plots also were surveyed in different years to account for inter-year density fluctuations. Censuses were carried out over 5-9 hours in dry and warm (19-25°C) weather. Surveys were interrupted at midday of hot days and during unfavorable weather (falling temperature, showers). Because all reptile species had low overall densities, differences in transect widths related to variation in habitat-specific ground cover (and hence observability of reptiles) were ignored. The total length of transects was 689.3 km (average – 7.5 km per 5x5 km square).

2.2.3. Topographic data

Altitudes and total coverage of landscapes (forest, open landscapes, mires, urban areas) within a circle of 2.5 km radius around each reptile observation were acquired from topographic maps (1996-1997) with scale 1 : 50 000. Degree of landscape fragmentation (average size of given landscape fragment) was also determined, but not used in analyses, because it had positive correlation with coverage in all cases ($p<0.05$). For each species, mean values of all observations in the same 5x5 km square were used. A random topographic sample was taken by determining altitudes in the center of each sampled 5x5 km square, and coverage of landscapes within a 2.5 km radius circle around the center of each 5x5 km square. In total, data were obtained for 12 squares occupied by *Lacerta agilis*, 89 - by *Zootoca vivipara*, 32 by *Anguis fragilis*, 15 by *Natrix natrix*, 18 by *Vipera berus*, and 92 random squares.

Differences between the random sample and reptile sites were evaluated by Mann-Whitney (Wilcoxon) W tests. In the case of significant altitude preferences for a species, only landscapes from the appropriate altitude range were compared.

2.2.4. Multiple regression analysis

Stepwise multiple regression (with F – to enter and remove variables at 4.0) was performed to assess relationships between relative abundance of reptiles, and the following predictors: climate factors, average human population density (from Turlajs, 1998), and proportion of different habitats along transects.

The distributions of four species (*Lacerta agilis, Anguis fragilis, Natrix natrix, Vipera berus*) were uneven, and their average densities on transects were very low (0.03-0.07 records per km). Therefore, relative abundance data for these species were expressed as the proportion of occupied 5x5 km squares in each 25x25 km plot. By contrast, *Zootoca vivipara* was observed in all 25x25 km plots (average abundance, 0.51 records per km); variation in density between years also was not statistically significant for this species (ANOVA, $p>0.1$). Thus, for *Z. vivipara*, relative density data in plots were used in analyses (records of juveniles were omitted to reduce seasonal differences).

Climate variables were acquired from published maps (Temnikova 1958, Kavacs 1998). Principal Component Analysis (PCA), with varimax rotation, was used for climate data reduction and to better capture environmental gradients (Brūmelis *et al.* 2000). The original variables were replaced by the smallest number of uncorrelated principal components (eigenvalue > 1.0) that encompassed 80 % or more of total variability. These principal components were then used as predictors in subsequent multiple regression analysis.

Data on habitats along transects were acquired from field descriptions. They were classified as follow:

- Deciduous trees (mostly *Betula spp., Alnus incana* L., *Populus tremula* L. dominated) stands – a) dry, and b) wet;
- Coniferous trees (*Pinus sylvestris* L., *Picea abiea* L.) stands – a) dry, and b) wet;
- Mires of various types (mostly bogs), including drained ones;
- Forest edges with open habitats, of various stands;
- Meadows and fallow lands, with or without sparse low shrub cover;
- Various agricultural landscapes (crops, gardens etc.).

Habitat data were square-root $(x+0.5)$ transformed (successful normalization in all but mire and agrolandscape types). Multicollinearity within the habitat data was low (one of 27 correlations at $p<0.05$, and two more at $p<0.1$). All statistics were performed with STATGRAPHICS Plus® program package. The distribution maps for *N. natrix* and *V. berus* in 1990-2005 were prepared using the personal data and the communications by biologists, naturalists and local people.

2.3. Results

2.3.1. Species Encountered

Five of the seven native species of reptiles were observed on transects in this survey. *Lacerta agilis* was found on 13 % of visited 5x5 km squares, *Natrix natrix* on 16 %, *Vipera berus* on 20 %, *Anguis fragilis* on 35 %, and *Zootoca vivipara* on 96 %. Two species were absent: the Pond Turtle *Emys orbicularis* is very rare (Ingelog *et al.* 1993), aquatic (Arnold, 2002), and possibly introduced (Čeirāns, unpublished data); the Smooth Snake *Coronella austriaca* also is very rare and confined to the coastal zone of western Latvia (see Chapter 5).

2.3.2. Analyses from topographic maps

In *N. natrix*, observed altitudes differed significantly from the random sample (p=0.00002, Fig. 2). This species was found only at elevations below 50 m a.s.l. Notable also was the absence of *V. berus* below 40 m a.s.l., although the elevation range of this species was not significantly different from that of the random sample.

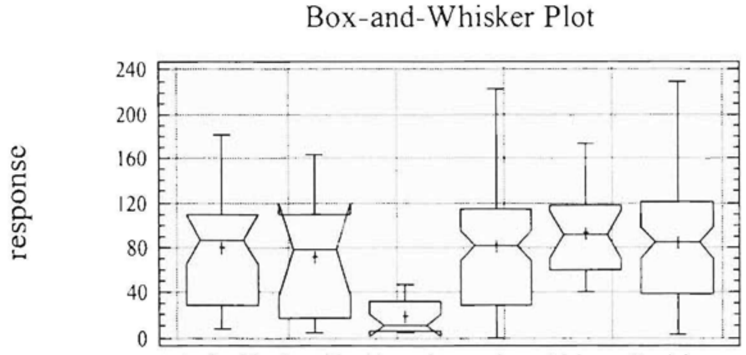


Figure 2

Altitudes of reptile observations and random sample (mean values marked with cross)

Two species had statistically significant landscape preferences. The landscapes inhabited by *A. fragilis* had higher forest coverage (range (%), mean ± SE, median: 36-95, 69±3, 70) and lower open landscape coverage (4-64, 26 ± 3, 26), than random sites (respectively: 1-97, 54 ± 2, 57; and 0-96, 41 ± 2, 39). These differences were significant at $p<0.01$. *Vipera berus* inhabited areas with higher coverage of mires (0-40, 8 ± 3, 2) than sites in the random sample (0-69, 4 ± 1, 0.05). The difference was significant at $p=0.03$. There were no differences in urban coverage between landscapes inhabited by reptiles and a random sample ($p>0.1$).

2.3.3.PCA on climate variables

PCA grouped climate variables in three components that accounted for 83 % of the total variance (Table 1). PCA 1 accounted for 47 % of the variance and had positive loadings from variables characterizing mild and short winters. PCA 2 (25 % of the variance) had positive loadings from variables characterizing high rates of precipitation and PCA 3 (12 %) from variables characterizing long and hot summers.

Table 1

Weight of climate parameters in PCA after Varimax rotation

Parameter	**Component 1**	**Component 2**	**Component 3**
Precipitation in warm (IV-X) season	-0.50	**0.81**	-0.07
Precipitation in cold (XI-III) season	0.22	**0.90**	-0.24
Annual precipitation	-0.07	**0.93**	-0.12
Days with snow cover	**-0.96**	0.13	0.05
Percentage of winters with unsteady snow cover	**0.90**	-0.12	-0.13
Air temperature in January	**0.93**	-0.13	0.27
Air temperature in July	-0.10	-0.47	**0.72**
Frost-free period on ground	**0.65**	-0.06	0.51
Frost-free period on grass	**0.94**	0.07	-0.12
Frost-free period in air	**0.75**	-0.08	0.23
Period with mean temp >10 °C	-0.18	-0.01	**0.84**
Period with mean temp > 5 °C	**0.86**	0.17	0.31
Sum of active temperatures	0.37	-0.24	**0.84**
Annual number of cloudy days	**-0.82**	0.31	-0.12

Bold - parameters with weight > 0.55, used in data reduction

2.3.4.Predictors of abundance

In the multiple regression analysis, reptile abundance was predicted only by climate and habitat factors. No relationships were found between reptile abundance and human population density. The latter varied between 6.0 and 23.5 (12.5±1.3) persons per km^2.

The abundance of *L. agilis* was predicted by a combination of two factors: climate (hot summers, PCA 3), and the proportion of dry coniferous forest, of which the more important was the habitat factor (R^2adj = 48%, DW = 2.20, $T_{PCA\ 3}$ = 2.50, T_{DryCon} = 3.25, p=0.0014).

The abundance of *Z. vivipara* was predicted mostly by habitat type and the influence of climate was somewhat less important. This species was most abundant in wet coniferous forests with cool summers (R^2adj = 36%, DW = 2.46, $T_{PCA\ 3}$ = -1.99, T_{WetCon} = 2.43, p=0.0086).

In three species, abundance was predicted by single factor. Abundance of *A. fragilis* was negatively related to the proportion of agricultural landscapes (R^2adj = 33%, p=0.0049, Fig.3). The abundance of the two snake species were both predicted by the same climate factor (PCA 1), but in opposite directions. *Natrix natrix* was more abundant in areas with relatively mild winters (R^2adj = 26%, p=0.013, Fig.4) and *V. berus* in areas with relatively cold winters (R^2adj = 20%, p=0.028, Fig.5). T_{WetCon} = 2.43, p=0.0086).

Because both snake species had restricted elevational distributions, the pronounced effect of climate on their abundance might simply reflect altitude (correlation between winter weather and altitude across plots, r = -0.84, p<0.0001) and thereby obscure effects of other factors. Therefore, I reduced the effect of climate by excluding plots outside the observed elevation range of the species; only plots from elevations above 40 m a.s.l. for *V. berus* (n = 14), and from elevations below 50 m a.s.l for *N. natrix* (n = 8) were selected for further analysis. At this scale, abundances of both species were positively related to various wet habitats: *N. natrix* – all wet forests and mires (R^2adj = 78 %, DW = 2.09, T_{Mire} = 2.65, T_{WetDec} = 2.97, T_{WetCon} = 3.84, p = 0.029), *V. berus* – wet coniferous forests and mires (R^2adj = 41 %, DW = 2.40, T_{Mire} = 2.10, T_{WetCon} = 2.40, p = 0.022).

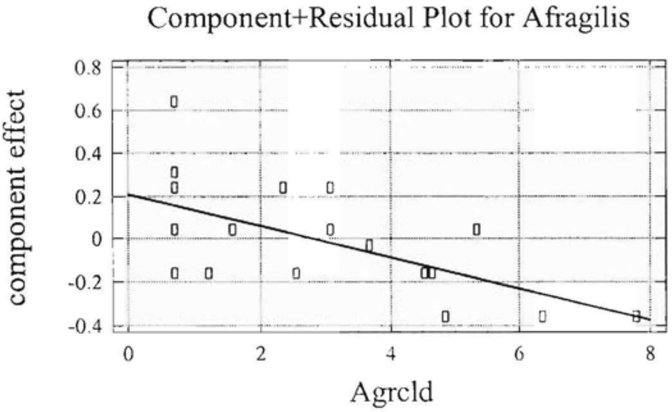


Figure 3

Relationship between the abundance of *A.fragilis* and the proportion of agricultural landscapes (p=0.0049)

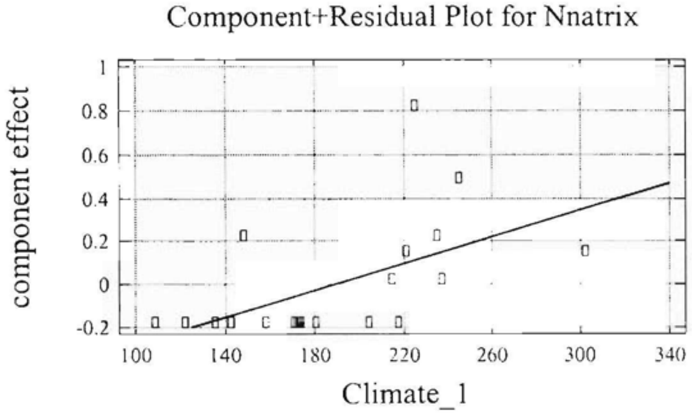


Figure 4

Relationship between the abundance of *N.natrix* and PCA 1 (mild winters; p=0.013)

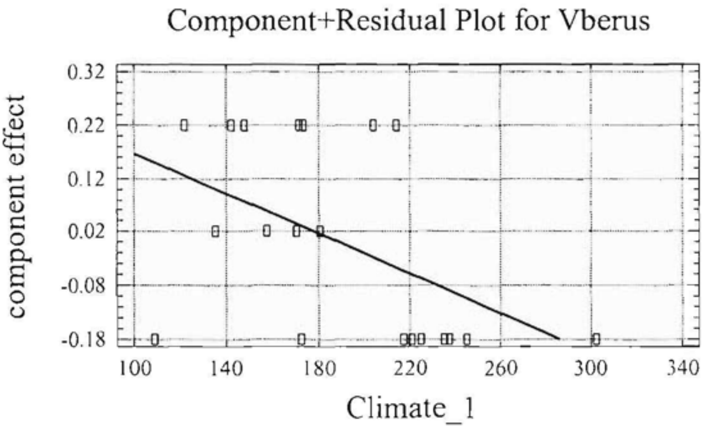


Figure 5

Relationship between the abundance of *V.berus* and PCA 1 (mild winters; p=0.028)

2.4.Discussion

In this study, I found significant effects of both habitat and climatic factors on abundance of reptiles in Latvia, but the particular effects varied among species. However, because given species may have different habitat and climate preferences in other climatic zone (e.g. Jablokov 1976, Pikulik *et al.* 1988), my conclusions, strictly speaking, apply only to the European sub-boreal forest zone and should be extrapolated to populations elsewhere with caution.

Abundance of snakes was affected mainly by winter weather, but in opposite directions in the two species. *Natrix natrix*, which is more abundant in areas with mild winters, is restricted in elevation in Latvia to areas below the 100 m isobar (Fig. 6), with only few records at elevations about 120 m a.s.l. This species is relatively common only in areas below 50 m. By contrast, *Vipera berus* is more abundant in areas with relatively harsh winters, more characteristic of uplands, and Eastern and Northern Latvia. In this survey, *V. berus* was not found in the Coastal Lowland, in spite of known records there (Fig. 7).

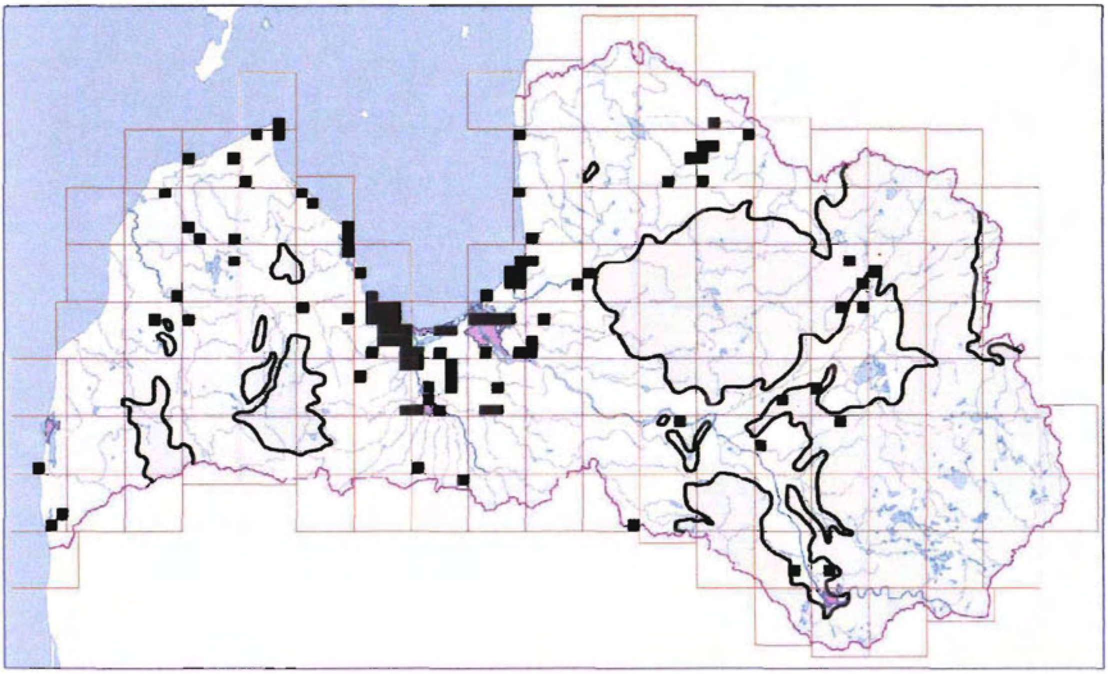


Figure 6

The distribution of *Natrix natrix* in 1990-2005 (solid squares), and the area above 100 m isobar (pale)

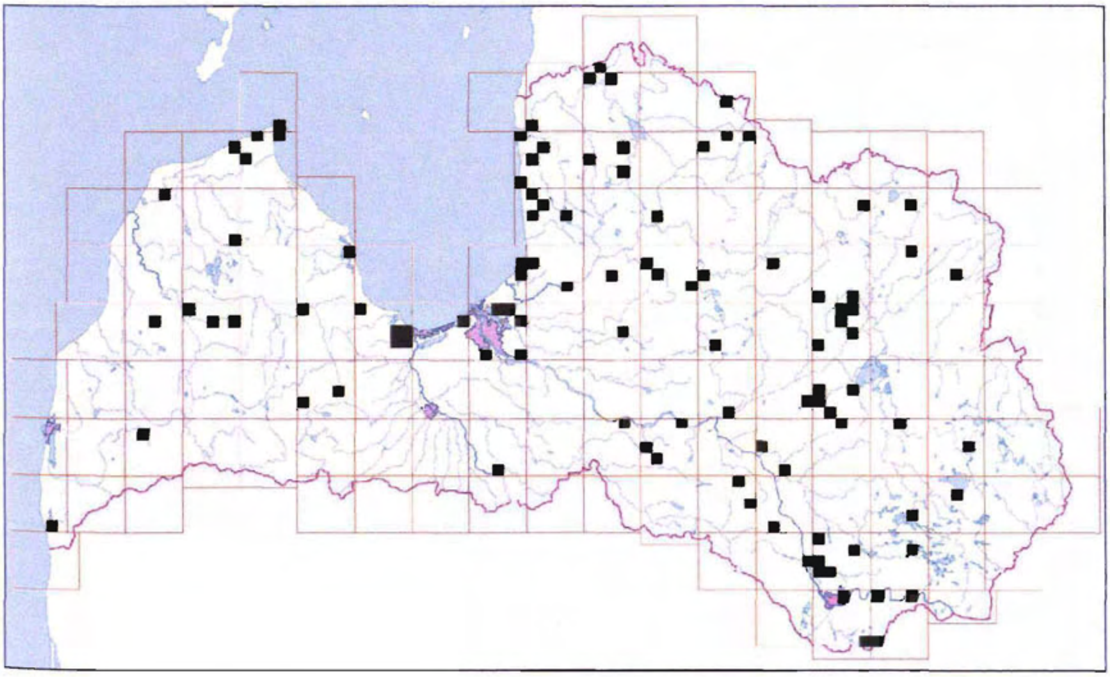


Figure 7

The distribution of *Vipera berus* in 1990-2005

Due to given abundance pattern, the latter species may face threats from global warming. There has been a distinct climate-warming trend in Europe during the 20th century, with a mean increase in annual temperatures of about 0.8 °C, but exceeding 3°C in some northern and central areas of European Russia. This warming event was exceptionally rapid during the 1980s, with increases of 0.25-0.5 °C per decade (IPCC, 2001). The recent climate change has had important ecological consequences for various organisms and ecosystems (Walther *et al.* 2002). As the temperature increase has been particularly evident during the winter period (IPCC 2001), climate warming could have a particularly adverse effect on *V. berus*. Although lack of data on numbers prevents firm conclusions about abundance trends in Latvia, there is indirect evidence of declines of *V. berus*, at least in some protected areas, since the 1980s (Čeirāns 2002b). This species prefers to hibernate in collective dens on slopes with southern exposure (Viitanen 1967, Prestt 1971), where the snow cover is less stable. Reduced snow cover in winter could cause a drastic increase in winter mortality of snakes due to freezing (Shine & Mason 2004). Thaws with following frosts would less likely happen in uplands with harsher climate, what possibly explains observed abundance pattern for *V. berus* in Latvia. Another contributing factor to increased winter mortality could be loss of fat reserves when hibernating temperatures are too high (Costanzo 1989). Low fat reserves post-hibernation also could negatively affect reproductive success (Prestt 1971). However, this factor would be less important in Latvia, because average winter temperatures there are still low.

Although habitat factors were not decisive for abundance of snakes at the regional scale, both species were more abundant in areas with higher proportions of various wet habitats. The connection of *N. natrix* with wet habitats is well known; such habitats are important for its main food resource - amphibians (Drobenkov 1995; Gregory & Isaac 2004). Mires and other wet habitats are regarded as typical for *V. berus* (Boshansky & Pishchelev 1978, Phelps 1978, Stumpel 1992, Zuiderwijk *et al.* 1998a), although not obligate (Belova 1976). Both species are versatile, have large home ranges, often with different wintering, mating, and summer grounds (Viitenen 1967, Prestt 1971, Phelps 1978, Madsen 1984). Hence, local factors such as prey abundance, presence of suitable egg-laying and wintering sites, topography etc. could be more important than broad habitat types like in the present survey.

In contrast to snakes, abundance of lizards in Latvia was affected by regional variations in both climate and habitat, especially the latter. The most important climatic factor was hot and long summer, which influenced abundance of lacertid species. With respect to habitat factors, abundance of the two lacertid species was positively influenced by coniferous forests and that of *A. fragilis* was negatively affected by agricultural landscapes.

Although the most significant regional factor for *L. agilis* in Latvia is presence of dry coniferous forest habitats, only parts of this broad habitat type are actually suitable. These are well-lit, open ecotopes of dry pine-dominant forests on sandy soils, and habitats created after their clearing, covered by grasses and undershrubs, interspersed with bare patches (Čeirāns 2002*b*; see also Chapters 3 and 4). Similar habitats on sand are typical for this species in the northern part of its range (House & Spellerberg 1983, Stumpel 1988, Berglind 2000). However, summer temperatures also are important. The highest densities of *L. agilis* were observed in South-Eastern Latvia, an area with a relatively continental climate.

Zootoca vivipara is very widespread and the most common reptile species in Latvia. It is found most often in areas with a high proportion of wet coniferous forest, which is verified by surveys done in forests (see Chapter 3). This species also is more abundant in areas with cool summers, but this factor is less important than habitat.

Habitat composition is a significant determinant of the abundance of *A. fragilis* in Latvia. This species is frequent in forested areas and rare in open ones, especially agricultural. The preference for more-or-less forested habitats is well known (Toporkova 1973, Stumpel 1985, Gruodis 1987, Pikulik *et al.* 1988). Within Latvian forests, *A. fragilis* prefers dry or artificially drained pine-dominated stands, and avoids damp stands and mires (see Chapter 3). Multiple regression analysis did not reveal a preference for dry coniferous forests, probably due to peculiarities of the wet coniferous forest type in the survey. This latter habitat type also included artificially drained stands, which are also good habitat for *A. fragilis* (see Chapter 3). *Anguis fragilis* was the only species of reptile in which an agricultural development adversely affected abundance. However, this species is still the second most abundant reptile in

Latvia and it is unlikely that agriculture poses a threat to its persistence, for several reasons. First, the density of the rural population in Latvia is relatively low (<15 inhabitants per km^2) and has been steadily decreasing since World War II due to a population flow into cities (Overview of the Latvian indicators of sustainable development, 2003). Second, the percentage of agricultural lands also has been declining since the 1940s (Berkgaute *et al.* 1999). Finally, pollutant emissions, loads of fertilizers and pesticides in Latvia are relatively low, and have decreased by 80-90 % since the early 1990s due to the economic depression following the collapse of the Soviet Union (Berkgaute *et al.* 1999, Fammler *et al.* 2000).

Other kinds of habitat loss or degradation are likely to be the biggest threats to most species of reptiles in Latvia. For example, the most important economic activity in many rural areas is timber harvesting, which increased two-fold between 1992 and 1997 (Berkgaute *et al.* 1999). However, harvesting is carried out mainly in mature stands, and for many reptile species its effect is positive rather than adverse, due to the creation of a more open mosaic habitat (Kutt 1993, Blouin-Demers & Weatherhead 2001, Lima *et al.* 2001). Raised bogs can be important habitats for some species and their loss can cause population decline (Phelps 1978, Stumpel 1992, Zuiderwijk *et al.* 1998a). However, peat extraction in Latvia has significantly decreased since the early 1990s, with about 70 % of bogs having been relatively untouched by human activities as recently as 1997 (Berkgaute *et al.* 1999). Some human activities in bogs, such as partial drainage, can even be beneficial for reptiles (see Chapter 3). Thus, although these anthropogenic factors may be important locally, they are not likely to cause a large-scale reptile declines in Latvia.

3. STAND COMPOSITION AND FOREST TYPE PREFFERENCES BY REPTILES IN THE ĶEMERI NATIONAL PARK AND THE GAUJA NATIONAL PARK

3.1.Introduction

Forest was the most characteristic European landscape feature beginning from the early post-glacial era, when about 80-90 % of the territory was forested, till the Middle Ages when large-scale deforestation commenced in the Central Europe. Presently, forest still covers about 312 million hectares (33 %) of Europe, mostly in the Nordic and East European countries (Stanners & Bourdeau 1994).

Unlike the Nordic Countries, where the intensification of forestry (e.g. using mechanization in forest planting and harvesting, the use of fertilizers, monoculture planting) resulted in considerable loss of biodiversity, the forests of East Europe have remained less affected (Stanners & Bourdeau 1994).

Therefore, reptile studies in East European forests are important from several aspects. The first is to gain an understanding of how widely reptiles exploit forest resources – the habitat that once dominated throughout the most of the range for many native species. The other stems from the species conservation aspect - after the collapse of the Soviet Union and establishing the market economy in the former socialistic countries, threats to biodiversity are increasing in this area. Thus, it is important to survey the role of forest resource diversity for reptiles.

All reptile species are ectoterms, and sun-exposure of the habitat is one of the key factors that determine site utilization (Heatwole 1977). The sun-exposure of the understorey in a forest depends on canopy features, such as species composition, canopy cover, stage of succession etc. Hence, the tree canopy in a forest strongly determines also the composition and structure of whole shrub and understory vegetation. For example, surface in coniferous forests has stabile sun exposure during a whole vegetation season. Surface in a pine forest usually is well lit, but in a spruce forest – shaded, and these forests have different understorey vegetation. Surface in a deciduous forest is subject to varying sun-exposure during a vegetation season, being well lit in spring, shaded in summer. As result, there are considerable seasonal changes in understorey vegetation (Priedītis 1999).

Information on reptile habitat preferences in the forests of East Europe is scanty, and mostly describes the density of reptiles in stands dominated by particular tree species (e.g. Belova 1976; Gruodis 1987; Pikulik et al. 1988). The main reasons for this lack of information are: i) low overall densities of reptiles in temperate forests (e.g. Jędrzejewska & Jędrzejewski 1998), and ii) use of mainly ephemeral microhabitats created by canopy gap disturbance (Greenberg 2001) and use of ecotops (e.g. Pikulik *et al.* 1988). In the Western Europe the role of forests as reptile habitats mainly is overlooked, with few exceptions (e.g. Spellerberg 1988).

The aim of the present study was to determine the general pattern of spatial distribution of reptiles among major groups of sub-boreal wooded habitats, and among tree stands with various composition and age. Bogs were also included in the study due to the gradual transition from raised bogs covered with sparse trees to wet forests. The survey was carried out in 1994-2000 in two different areas – the Ķemeri National Park and the Gauja National Park, and the State Forest Service databases for these territories were used to study tree stand parameters essential for reptiles.

3.2.Materials and methods

3.2.1.Study areas

Ķemeri National Park (KNP) is located south-southwest from the Gulf of Riga. The total area is 42,790 ha; forests occupy 51 %, mires 24 %, waters 10 %, agricultural lands and shrubs 12 % and human settlements 3 % of the territory. Altitude ranges from 0 to 72 m a.s.l, sum of active temperatures 1850-2000 °C, annual precipitation 700-800 mm (Kavacs 1995, 1998). Forest habitats are very diverse, containing the full range of forest types found in Latvia (Latvian Fund for Nature, unpublished).

Gauja National Park (GNP) is located in north-central Latvia. The total area is 91,745 ha, forests occupy ~ 50 %, agricultural areas and human settlements ~ 40 % of the territory, mires are few in number and extension. Altitude in the GNP ranges from 25 to 174 m a.s.l., sum of active temperatures is 1800-1900 °C, annual precipitation 700-800 mm, and upland forests dominate in the area (Kavacs 1995, 1998).

3.2.2. Habitat classification

Latvia has a unique system of forest typology that does not emphasize phytosociological methods, but focuses on site quality of particular land-types (Avis 1997). Hence this typology is designed manly for forestry purposes. There are five major forest types groups depending on water regime and trophic level, subdivided further into 23 growth condition types on the basis of their position along a nutrient and floral species composition gradient, from poor (oligotrophic) to rich (eutrophic) stands. Wet forests are divided in two groups: forests on mineral soil (periodically wet, roots of trees reach underlying mineral soil), and forests on wet peat (roots do not reach mineral soil). Similarly, drained forests are also divided into forests on drained mineral and drained peat soil (Bušs 1997). There is a gradual transition with increasing paludification from pine forest on *Sphagnum* peat to raised bog (association *Sphagnion magellanici*, after Kabucis 2000), where the role of moss in biomass accumulation is more important than the role of trees (Bušs 1997). Characteristics of 20 surveyed forest types are shown in Appendix 1.

Unlike forest typology, the syntaxonomical classification of Latvian forests has not been fully developed yet, and it is attributed only to natural forests. It has some similarity with forest typology, especially regarding upland pine forests, where three types (Cladinoso-callunosa, Vacciniosa, Myrtillosa) are coherent with plant associations. However, there are many substantial differences from forest typology also. Thus, the same plant association can be found in several forest types (in wet pine forests, for example), or several associations can be found in one forest type, especially regarding deciduous and spruce forests (Aegopodiosa, Myrtilloso-polytrichosa, Dryopteriosa, Filipendulosa types) (Priedītis 1999).

Hence forest typology is the only forest classification system that covers the whole variety of Latvian forests. Therefore, the forest type was chosen as a basic habitat unit for further analyses in the present survey. In the present analysis two wet pine forest types (Sphagnosa, Caricoso-phragmitosa) were combined in one unit, because they belong to same plant association (Vaccinio uliginosi-Pinetum) (Priedītis 1999). Additionally, raised bogs are also included in analyses as a separate habitat.

3.2.3. Data base of the State Forest Service

Forest data bases are created by professionals during inventory of forest stands for forestry purposes. Forest inventory was carried out in the Ķemeri National Park in 1989 and in the Gauja National Park mainly in 1987-88 (some territories were inventorized in 1994). The data base is supplemented by forest plans at scale 1 : 20 000. The forest is divided into stands with uniform growth conditions and tree stand features. The area occupied by a stand varied from less than 0.5 ha to more than 15 ha.

Only a few stand parameters from the forest databases appeared to be useful for the present scientific purposes. Some of the parameters, such as standing volume, origin of stand etc., are useful mainly for forest management. The mean heights and diameters of trees indicated in database are misleading (especially regarding young stands) due to the long time span between the inventory of stand and reptile observations (5-8 years for KNP, and 5-13 years for GNP). However, the age of stand can be calculated from the database, and the tree species composition of the stand from the database can be used with a sufficient level of confidence.

Usual practice is that the mean age of stands has been determined from cores bored from the root neck in several medium sized trees (Brice 1998). The stand composition in the data base is characterized by a code, where each tree species has a coefficient (an integer between 1 to 10) proportional to the stock of each species in the stand. The tree species for which storage is less than 5 % are not included in the formula. The sum of coefficients of all components is 10 (Brice 1998). In present analysis, coefficients for all deciduous species were pooled.

3.2.4.Transects

Data were collected on transects in the field seasons (later April to early September) of 1994-1997 for the Ķemeri National Park (KNP), and 1998-2000 for the Gauja

National Park (GNP). Transects were evenly distributed and covered the whole territory in both study areas. The total lengths of transects were 198.1 km in KNP and 103.7 km in GNP. Eighteen forest and raised bog types were documented in KNP, and 11 in GNP. All but three of forest types found in Latvia were covered by transects in one or the other study area, and these were the relatively rare types (Bušs 1997): periodically wet sparse pine forests on very poor sandy soil (Callunoso-sphagnosa), post-drained Callunoso-sphagnosa type (Callunosa mel.), and wet black alder forests on woody peat in sites with abundant calcareous groundwater flow (Filipendulosa) (see Table 7 in Results).

Censuses were carried out once on each transect, for 5-9 hours under dry and warm weather conditions. They were located in forest habitats, mostly in sites with potentially highest reptile density (forest ride verges, cuttings et.). Each observation of a reptile was mapped at a scale 1: 50 000, and a brief description of the site was made. Each description was later compared with forest management plans and stand descriptions from the database of the State Forest Service, to ensure coherence between both the find and the database. Observations on forest fringes and sides of large roads were excluded from analysis as not representing a forest environment. Observations of juveniles were also omitted to reduce seasonal variation in density. Forest types along transects was determined from the forest database.

Table 2

Number of forest stands analysed in the Ķemeri National Park (KNP) and the Gauja National Park (GNP)

Forest stands in sites of records of	**KNP**	**GNP**
Anguis fragilis	14	8
Zootoca vivipara	28	21
Natrix natrix	22	3
Random stands	200	200

3.2.5.Data analysis

I used randomly selected stands from the State Forest Service database (200 for each of the study area) as random sites for comparison with stands inhabited by reptiles (Table 2). Data set for *N. natrix* from the Gauja National Park was too small for separate analysis, and it was used only in the analysis of the variation of preferred habitats during a season.

Differences in age and composition of tree stands were assessed by non-parametric Mann-Whitney (Wilcoxon) test. Linear regression analysis was performed to test the relationship between age and part of various tree species in the various stands. Polynomial regression analysis was used to test the statistical significance of relationship between reptile observation date and stand composition, fitting of second and third order polynomial model was tested.

Deviation (*D*) from the expected proportion of records in each forest type was calculated by a simple formula:

$$D = (O-E) / E,$$

where *O* is the observed proportion of records (%), and *E* the forest type proportion (%) on the transects. Values are between −1 and 0, if a species avoids a particular habitat and > 0 if a habitat is preferred. There is no applicable statistical method to test the significance of this deviation (*D*). However, the representativeness of a given transect in a particular forest should correspond to the length of the transect due to low overall density of reptiles in temperate forests (Jędrzejewska & Jędrzejewski 1998, present survey). Hence, the significance of the deviation (*D*) was evaluated by transect length with the most plausible results for transect lengths of more than 10 km, and the least plausible results for transects of less than 2 km.

Two formulas were used to evaluate the species niche breadth in forests. In the case of wide niche breadth, the proportional exploitation of all forest types was to be expected. The sum of absolute numbers from deviations of expected record proportions (observed proportion (%) of record minus forest type proportion) approaches 0 in case of total correspondence and 200 in case of total discrepancy with the distribution of forest types on site. Therefore niche breadth (*NB*) could be expressed by the formula:

$$NB = 1 - [\sum_{i=1}^{n} (O - E)] / 200$$

with values ranging from 1 (equal exploitation of all forest types) to 0.

Levin's measire of niche breadth (NB_{Levins}) was also calculated (Krebs 1989):

$$NB_{Levins} = 1 / \sum_{i=1}^{n} p_i^2,$$

where p_i is the proportion of records in the i^{th} forest type of n forest types. The percentage overlap (P_{jk}) and Hurlbert's index of niche overlap (L) (Krebs 1989) were used to evaluate the habitat overlap between reptile species.

The percentage overlap was calculated as:

$$P_{jk} = \sum_{i=1}^{n} (\min p_{ij}, p_{ik})\ 100,$$

and the Hurlbert's index as:

$$L_{jk} = \sum_{i=1}^{n} (p_{ij}\, p_{ik} / a_i),$$

where p_{ij}, p_{ik} are the proportion (%) of records in the forest type i for the species j and k, and a_i - the proportion of i forest type on transects.

Regression analysis was performed to test the relationship between transect length and number of records in the forest type. All Statistical analyses were performed using Microsoft© STATGRAPHICS Plus 2.1® software.

3.3.Results

A total of 149 reptile records were counted (86 in KNP, 63 in GNP). Two species – *Anguis fragilis* and *Zootoca vivipara* – out of five were regularly found in both study areas. As to *A. fragilis* records, mean density was the same in both of study areas (0.08 records per km), while in *Z. vivipara* the mean density was more than two times higher for GNP than for KNP (0.48 and 0.21 records per km, respectively). Density in the latter was higher for most of the forest types, most likely due to differences in the activity of the species between years of data collection (1994-97 for KNP and 1998-2000 for GNP). *Natrix natrix* was common in forests in KNP (0.13 records per km), but not in GNP (0.03 records per km), reflecting its uneven distribution and rarity. Two species – *Lacerta agilis, Vipera berus* - were rare in both areas (densities 0.01 or less records km^{-1}) and, although their habitat preferences were not analysed, some data are discussed in Chapter 3.4.

3.3.1.Composition and age of forest stands

Although stands inhabited by *A. fragilis* were older than randomly chosen (Table 3), the differences were not significant in both areas ($p>0.1$). Pine (*Pinus sylvestris*) was the dominant species in the habitats of *A. fragilis* (Tables 4-5), where it had higher relative abundance than in the random stands (KNP $p=0.02$, GNP $p=0.04$). Spruce (*Picea abies*) and deciduous trees usually had low relative abundances in *A. fragilis* habitats.

Forest stands inhabited by *Z. vivipara* were younger than randomly chosen sites. These differences were significant in one area (KNP, $p=0.01$), but not in the other ($p>0.1$). Concerning its habitat preferences species also behaved different in the two study areas. In the Gauja National Park pine strongly dominated in the habitats (Table 5), and such stands were preferred over others ($p=0.03$). In the Ķemeri National Park, *Z. vivipara* habitats were more variable, and their composition was correlated to the age of stand (Table 4). Old spruce-dominated stands were avoided (Figure 8). Correspondingly, the proportions of pine and deciduous trees tended to increase in mature stands inhabited by Z. *vivipara*. Deciduous tree stands were avoided comparing with random sites ($p=0.004$).

There were no differences in age of tree stands between habitats of *N. natrix* and randomly chosen sites ($p=0.29$), and species did not show a preference for a tree species. Young deciduous stands were avoided by *N. natrix* (Figure 9). Unlike two previous reptile species, *N. natrix* often inhabited stands with a large proportion of deciduous trees.

The most important deciduous component in all stands was birch (*Betula pendula, B. pubescens*) while other deciduous tree species (*Populus tremula, Quercus robur,* *Alnus glutinosa, Fraxinus excelsior, Salix sp., Alnus incana, Ulmus sp.*) were less common. Differences with stand composition of random sites for separate deciduous species in all cases were not significant.

Table 3

Age (in years) of forest stands inhabited by *Anguis fragilis, Zootoca vivipara, Natrix natrix*, and of random stands (mean ± standart error, range in parentheses)

Forest stands in sites of records of	**KNP**	**GNP**
Anguis fragilis	81.4±5.4 (47-112)	95.1±15.6 (37-164)
Zootoca vivipara	59.6±6.5 (10-147)	70.4±7.0 (15-114)
Natrix natrix	68.6±4.4 (24-97)	---
Random stands	70.8±2.2 (7-182)	79.2±2.4 (13-194)

Table 4

Ķemeri National Park. Stand composition (coded by formula from the database of the State Forest Service) and correlation between the proportion of various stand components and the age of the stands (*r, p*) in places inhabited by reptiles, and in random sites. ** - significant at p < 0.05; * - significant at p < 0.1

Habitat of	**Tree species**	**Mean ± Standard Error**	**Range**	***r***	***p***
Anguis fragilis	Pine	6.43±0.97	0-10	0.10	0.75
	Spruce	1.36±0.55	0-6	-0.07	0.80
	Deciduous trees	2.21±0.76	0-9	-0.07	0.81
Zootoca vivipara	Pine	5.14±0.74	0-10	0.47**	0.01
	Spruce	3.29±0.76	0-10	-0.65**	0.0002
	Deciduous trees	1.57±0.39	0-8	0.37*	0.05
Natrix natrix	Pine	4.68±0.87	0-10	-0.19	0.39
	Spruce	1.55±0.50	0-10	-0.26	0.23
	Deciduous trees	3.77±0.73	0-10	0.41*	0.06
Random stands	Pine	4.13±0.28	0-10	0.29**	0.0000
	Spruce	1.95±0.19	0-10	-0.26**	0.0002
	Deciduous trees	3.92±0.26	0-10	-0.12*	0.09

Table 5

Gauja National Park. Stand composition (coded by formula from the database of the State Forest Service) and correlation between the proportion of various stand components and the age of the stands (r, p) in places inhabited by reptiles, and in random sites. ** - significant at $p < 0.05$; * - significant at $p < 0.1$

Habitat of	**Tree species**	**Mean ± Standard Error**	**Range**	***r***	***p***
Anguis fragilis	Pine	8.75±0.37	7-10	-0.54	0.17
	Spruce	0.86±0.35	0-2	0.58	0.13
	Deciduous trees	0.38±0.18	0-1	-0.04	0.13
Zootoca vivipara	Pine	7.00±0.79	0-10	0.05	0.83
	Spruce	0.86±0.37	0-7	0.06	0.74
	Deciduous trees	2.14±0.63	0-8	-0.11	0.65
Random stands	Pine	5.16±0.29	0-10	0.17**	0.02
	Spruce	1.67±0.19	0-10	0.06	0.43
	Deciduous trees	3.17±0.25	0-10	-0.22**	0.003

3.3.2.Seasonal variations in stand preferences by reptiles

Microclimatic conditions on the ground surface may differ depending on canopy composition. Hence, seasonal variations in habitat preferences by reptiles can be expected. In this respect, I observed monthly variations in the mean proportion of stand components (Figures 10-12). The data set was too small for separate analysis for each of study areas, and data from both were combined.

All three reptile species showed two peaks – (i) spring and (ii) end of summer/autumn for the selection of pine-dominated stands. The relationship between the relative abundance of pine and the date was relatively weak, but statistically significant for *A. fragilis* and *Z. vivipara* (Table 6). Spruce was at maximum in *Z. vivipara* summer habitats; this relationship was weak, but significant. No distinctive pattern regarding the presence of spruce in a habitat was found in two other reptile species. There was no evidence of better utilization of deciduous stands by reptiles in spring, when the forest ground is well lit. Moreover, in the meteorological summer month June, the average proportion of deciduous tree stands utilized as habitat by *A.* fragilis was higher than in the May; this relationship was relatively weak, but significant. A similar trend (but statistically not significant) was observed in *N. natrix* habitats.

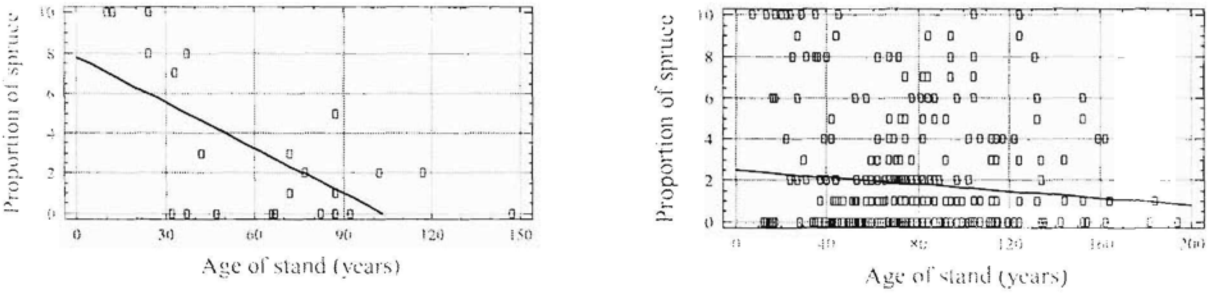


Figure 8

Relationship between the proportion of spruce in the stand and the age of the stand for: (left) stands utilized by *Zootoca vivipara* ($r = -0.48$; $p = 0.0005$), and (right) random stands ($r = -0.10$; $p = 0.05$). (In both figures combined data from the Ķemeri National Park and the Gauja National Park were used)

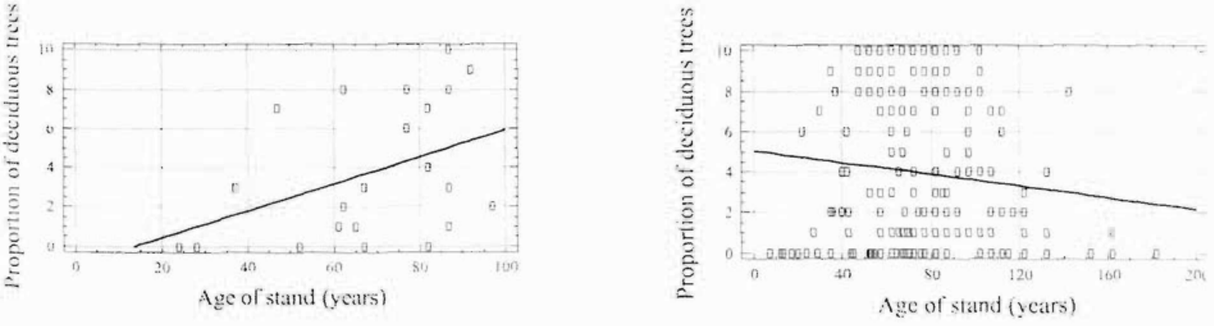


Figure 9

Relationship between the proportion of deciduous tree species in the stand and the age of the stand in the Ķemeri National Park for: (letf) stands utilized by *Natrix natrix* ($r = 0.41$; $p = 0.06$), and (right) random stands ($r = -0.12$; $p = 0.09$).

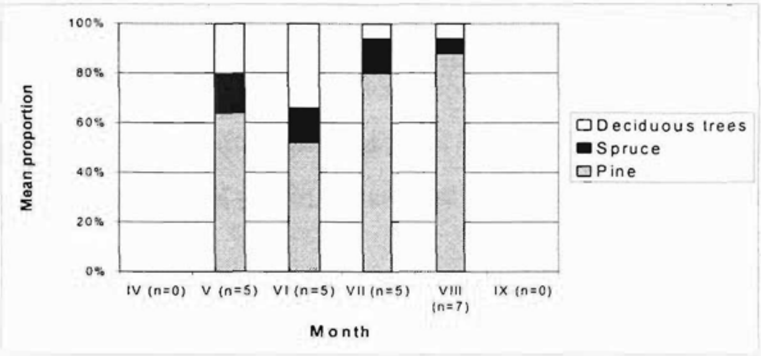


Figure 10

Monthly variation in the composition of the stands of trees utilized by *Anguis fragilis*

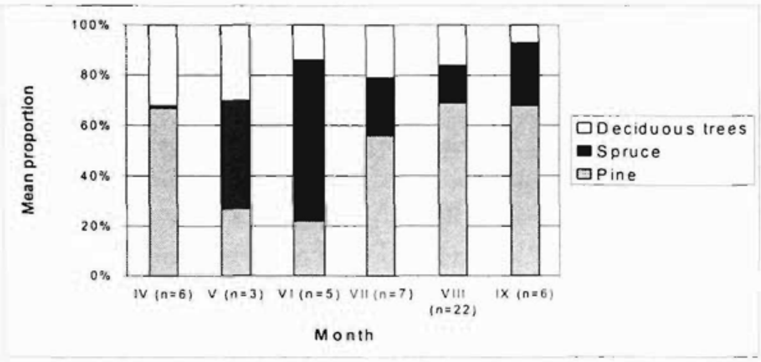


Figure 11

Monthly variation in the composition of the stands of trees utilized by *Zootoca vivipara*

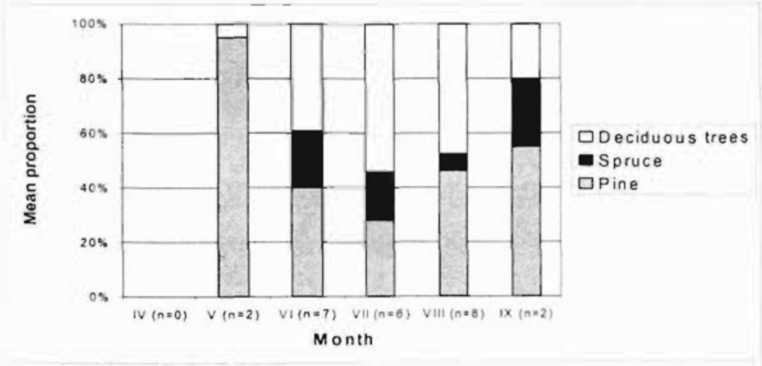


Figure 12

Monthly variation in the composition of the stands of trees utilized by *Natrix natrix*

Table 6

Statistical significance (p) in the relationship between proportion of tree species in the reptile habitat and reptile observation date. For each reptile species indicated: fitting at second order polynomial model (R^2 in the first row), and fitting at third order polynomial model (R^2 in the second row). ** - significant at $p < 0.05$; * - significiant at $p < 0.1$.

Forest stands in places of records of	**Pine**	**Spruce**	**Deciduous trees**
Anguis fragilis	R^2=0.20, p=0.13 R^2=0.36*, p=0.06	R^2=0.07, p=0.50 R^2=0.08, p=0.70	R^2=0.15, p=0.22 R^2=0.34*, p=0.05
Zootoca vivipara	R^2=0.08, p=0.16 R^2=0.17**, p=0.04	R^2=0.05, p=0.29 R^2=0.25**, p=0.005	R^2=0.05, p=0.35 R^2=0.06, p=0.40
Natrix natrix	R^2=0.13, p=0.22 R^2=0.14, p=0.35	R^2=0.002, p=0.98 R^2=0.10, p=0.54	R^2=0.14, p=0.19 R^2=0.14, p=0.35

3.3.3.Forest type preferences

The correlation between the number of *A. fragilis*_records and the transect length by forest types was not significant for KNP (R^2 = 9.5 %, p = 0.21) and positive for GNP (R^2 = 70.3 %, p = 0.001). *Anguis fragilis* was found more often than expected in two groups of forest types (Table 7). Of the dry upland forests it preferred pine-dominated types on fairly poor to moderately rich soil (Vacciniosa, Myrtillosa). Data regarding mesotrophic forests of Hylocomiosa type were discrepant. There were large percentages of *A. fragilis*_observations in these forests for both of the study areas (KNP – 26.7 %, GNP – 37.5 %). However, in KNP the number of observations was higher than expected, but in GNP – lower than expected. Hylocomiosa is a forest type where both – pine or spruce can be dominant (Bušs 1997). *Anguis fragilis* prefers pine stands (see above). Therefore, the discrepancy probably resulted from differences in Hylocomiosa canopy composition between both areas. Among the drained forests, *A. fragilis* preferred pine, pine – spruce forests on mesoeutrophic soil, both on mineral soil and peat (Myrtillosa mel. and turf. mel). The herb layer in these forest types is similar to those of upland mesotrophic pine, pine-spruce forests (Bušs 1997). The species was totally absent in all wet forest types, raised bog and several drained types.

In *Zootoca vivipara*, there was a significant positive correlation between the number of records and the length of transect in a forest type for both study areas (KNP: R^2 = 45.2 %, p = 0.002; GNP: R^2 = 79.1 %, p = 0.002). However, forest type preferences are similar in both areas (Table 7). The species was present in most types of dry upland forests. However, the number of observations was lower than expected in most of the cases.

Table 7

Transect length (*TL*) within forest types and deviation (*D*) from the expected proportion of records for reptiles in Ķemeri National Park (KNP) and Gauja National Park (GNP). Length of transects: no asterisk – less than 2 km; * - 2-5 km; ** - 5-10 km; *** - more than 10 km. NF – no reptile records on transect.

Forest type	**TL (km)**		***Anguis fragilis***		***Zootoca vivipara***		***Natrix natrix***
	KNP	**GNP**	**KNP**	**GNP**	**KNP**	**GNP**	**KNP**
Upland (dry)							
Cladinoso-callunosa	11.2	1.1	NF***	NF	-0.58***	NF	NF***
Vacciniosa	9.8	1.7	0.35**	14.24	-0.52**	3.88	NF**
Myrtillosa	19.2	31.8	0.38***	0.22***	NF***	-0.28***	-0.21***
Hylocomiosa	18.2	46.3	1.90***	-0.16***	-0.22***	-0.15***	-0.16***
Oxalidosa	-	9.3	-	NF**	-	-0.55**	-
Aegopodiosa	-	2.3	-	NF*	-	NF*	-
Wet mineral soil							
Vaccinioso-sphagnosa	3.9	-	NF*	-	NF*	-	NF*
Myrtilloso-sphagnosa	13.4	0.6	NF***	NF	0.41***	2.49	1.34***
Myrtilloso-polytrichosa	1.5	-	NF	-	NF	-	NF
Dryopteriosa	2.9	-	NF*	-	NF*	-	1.64*
Wet peat soil							
Raised bog	16.1	5.6	NF***	NF**	1.64***	1.22**	-0.53***
Sphagnosa, Caricoso-phragmitosa	29.4	2.8	NF***	NF*	0.45***	3.44*	-0.74***
Dryopterioso-caricosa	9.4	0.5	NF**	NF	NF**	NF	-0.19**
Drained							
Callunosa turf. mel	2.2	-	NF*	-	NF*	-	5.93*
Vacciniosa mel.	0.9	-	NF	-	NF	-	7.57
Vacciniosa turf. mel.	2.9	1.7	3.57*	NF	2.26*	0.22	6.90*
Myrtillosa mel.	11.1	-	3.76***	-	1.13***	-	-0.31***
Myrtillosa turf. mel.	18.3	-	0.44***	-	0.80***	-	-0.58***
Mercurialiosa mel.	13.3	-	NF***	-	-0.65***	-	-0.43***
Oxalidosa turf. mel.	14.4	-	-0.08***	-	NF***	-	1.65***

The only exception (Vacciniosa type, GNP) should be considered as occasional because of small length of transect here. *Zootoca vivipara* preferred several forest types from the group of wet forests. Typical habitats were stunted pine stands on raised bog that form a gradual transition to pine, pine-birch forests (Sphagnosa, Caricoso-phragmitosa) on wet *Sphagnum* and *Carex* peat, and also include partially drained areas (Vacciniosa turf. mel. type). The species also showed preference for forests on moderately rich soils with mixed canopy composition and a *Vaccinium myrtillus*_– dominated herb layer, in cases when they were not too wet nor completely dry. These were periodically wet (Myrtilloso-sphagnosa) or drained (Myrtillosa mel., Myrtillosa turf. mel.) forest types. *Zootoca vivipara* was absent or found less than expected in all types of forests on rich soil where deciduous trees and spruce dominated the canopy.

The correlation between the number of *N. natrix*_records and the transect length in forest types was not significant (KNP: $R^2 = 2.5$ %, p = 0.53). The species was observed in a wide variety of forest types (Table 7), being absent only in the driest pine forest types (Cladinoso-callunosa, Vacciniosa) and in two wet forest types (Vaccinioso-sphagnosa, Myrtilloso-polytrichosa) with relatively small transect length. *Natrix natrix* preferred periodically wet or drained forests, where it was typical for several types with mixed (pine-spruce-deciduous tree) canopy composition (Myrtilloso-sphagnosa) or with a spruce and deciduous tree canopy (Oxalidosa turf.mel.). The species was also frequent in drained pine forests on poor *Sphagnum* and *Carex* peat (Callunosa turf.mel, Vacciniosa turf.mel.), around flooded peat mines in raised bogs. However, their pre-drained forest types (Sphagnosa, Caricoso-phragmitosa) and active raised bogs were avoided.

3.3.4.Habitat niche breadth and overlap

Habitat niche breadth index (NB) was higher than Levins's index (NB_{Levins}) in GNP and lower in KNP (Table 8). However, the latter index may not be representative (see discussion). Two of the reptile species surveyed occupy wide habitat niches in forests: *Zootoca vivipara* can be regarded as the most generalized species among them, but while *N. natrix* tends to inhabit moist forest. Data for the later species in GNP may not be representative due to small number of observations there (n=3). The third species - *Anguis fragilis* prefers dry habitats (see above) that narrow its niche in wet areas such as KNP.

Niche overlap between the three most common forest reptile species was relatively high for both the percentage and Hurlbert's indexes (Table 9). Remarkable was the high value of the latter index for *A. fragilis* with both, *Z. vivipara* and *N. natrix*, in KNP. An index value of > 1 indicates the trend of similar habitat use between two species, that in the case of the *A. fragilis* – *N. natrix* pair was unexpected. However, this result was mainly due to the overlap of habitats in the drained, not natural forests. In detail, 75 % of the value of Hurlbert's niche overlap index in the *A. fragilis* – *N. natrix* pair, and 81 % in the *A. fragilis* – *Z. vivipara* pair (and only in 55 % in the *Z. vivipara* – *N. natrix* pair) originated from the niche overlap in the drained forests, although they occupied only 32 % of the transect length.

High niche overlap in the percentage index between *A. fragilis* and *Z. vivipara* in the Gauja National Park probably was associated with two factors: i) a large proportion of the dry forest (89 %) suitable for the former, and ii) wide use of various habitats (including dry forests) by the latter. The third forest species, *Natrix natrix*, is rare and unevenly distributed in this area.

Table 8

Habitat niche breadth (NB) and Levin's niche breadth (NB_{Levins}) for reptile forest types of Ķemeri National Park (KNP) and Gauja National Park (GNP)

Species	KNP		GNP	
	NB	NB_{Levins}	NB	NB_{Levins}
Anguis fragilis	0.47	5.2	0.70	2.8
Zootoca vivipara	0.60	6.6	0.76	4.3
Natrix natrix	0.57	9.7	0.62	1.8

Table 9

Indexes of reptile forest type niche overlap (percentage / Hurlbert's) in Ķemeri National Park (KNP; lower left of array) and Gauja National Park (GNP; upper right of array)

	Anguis fragilis	*Zootoca vivipara*	*Natrix natrix*
Anguis fragilis	-	68 / 1.59 (GNP)	33 / 0.28 (GNP)
Zootoca vivipara	41 / 1.26 (KNP)	-	33 / 0.28 (GNP)
Natrix natrix	38 / 1.27 (KNP)	42 / 0.96 (KNP)	-

3.4.Discussion

Three reptile species (*A. fragilis, Z. vivipara, N. natrix*) were common in the surveyed forests. These species are the dominant reptiles in the Białoweža Primeval Forest, where their records constituted 96 % of all reptile observations (Jędrzejewska & Jędrzejewski 1998). The proportion of records for each reptile species in the Ķemeri National Park was similar to those of the Białoweža Forest (Table 10). Therefore, the reptile communities in both can be considered as typical for northern nemoral - southern sub-boreal forests. In Gauja National Park one species (*N. natrix*) was rare, probably due to unfavorable climate conditions.

Table 10

Percentages of reptile species records in two National Parks of Latvia (present survey) and the Białoweža Primaeval Forest National Park of Poland and Belarus (Jędrzejewska & Jędrzejewski 1998)

Species	Kemeri National Park	Gauja National Park	Białoweža Primaeval Forest
Anguis fragilis	18	12	11
Lacerta agilis	2	2	1
Zootoca vivipara	49	79	52
Natrix natrix	30	5	33
Vipera berus	1	2	3
Total	100	100	100

The observed distribution of *A. fragilis* within forests can largely be explained by the moisture conditions as it avoids wet forests and raised bogs. The species was, however, observed in degraded bogs on sites with drained pine - birch forests (Vacciniosa turf. mel.) around old saturated peat mines. In contrast, the absence of *A. fragilis* in the driest forest type (Cladinoso-callunosa) can be explained by insufficient water supply in the habitat. Another important factor is the preference of pine-dominated stands, over spruce or deciduous tree dominated forest types both upland (e.g. Oxalidosa) and drained (e.g. Mercurialiosa_mel.). The only record of *A. fragilis* in drained spruce-deciduous forest (Oxalidosa turf. mel.) may be explained by migration from neighboring pine stands. The species is referred to be quite sedentary, with a home range of 250-400 square meters (Spellerberg 1988). There was weak relationship between observation date and canopy composition (Table 6), and hence, however, some migration between habitats can be suggested. The species was found in average older stands in than random samples, although the differences were no statistically significant. Considering also the sedentary habit of *A. fragilis,* this may indicate that the species is more sensitive to habitat disturbances than are other reptiles. The pattern observed in Latvia is verified by descriptions of the *A. fragilis* forest habitats in Lithuania (Gruodis 1987) and Northern Belarus (Pikulik *et al.*_1988). The herb layer described for *A. fragilis*-inhabited conifer plantations in Netherlands (Stumpel 1985) also is similar to that described for dry pine forest types in Latvia (Bušs 1997).

Zootova vivipara generally avoided spruce-dominated stands that were more than 40 years old, and such stands were well represented at the study areas (Figure 8). The only exception was in a stand bordering with pine-dominated stand. Young spruce stands, which are often been thinned out to produce higher wood volume from each tree (Brice 1998), are good *Z. vivipara* habitats until canopy closure. At the age of 35-45 years spruce is about 10-15 m high with a mean stem diameter of 11-16 cm at 1.3 m height (data from the State Forest Service database). At these ages, stands become too shaded to sustain *Z. vivipara* populations. The positive effect of stand thinning in forests has been observed for heliothermic lizards in Australia (Kutt 1993) and South America (Lima *et al.* 2001). Spruce was far more typical for *Z. vivipara* habitats in KNP than in GNP. In a random data set, the proportion of spruce dominated stands that were younger than 40 years was 5.0 % from all stands in the former and 2.2 % in the latter. Hence differences between both study areas could result from the rarity of young open spruce stands suitable for Z. *vivipara* in the Gauja National Park.

Regarding forest type preferences, the number of Z. *vivipara* observations was less than expected in dry upland pine, pine-spruce forests. However, Z. *vivipara* records in these forests still formed a considerable part of all records in GNP (68.0 %), but not in KNP (9.5 %)). Data from the present study suggest that in Latvia Z. *vivipara* prefers forests with considerable pine presence in the canopy, and with some extra soil moisture that persists even in drained stands. In the southern and eastern parts of boreo-nemoral forest zone, utilization of deciduous stands by Z. *vivipara* is more usual (Pikulik *et al.* 1988; Dunajev & Haritonov 1989). In the northern Belarus, the average density of Z. *vivipara* in deciduous forests was observed to be 3 - 4 times lower than in pine forests (Pikulik *et al.* 1988). In central Belarus Z. *vivipara* inhabited deciduous stands, but avoided dry pine forest. Pine forests there were utilized by L. *agilis* (Pikulik *et al.* 1988). Similarly, some regional variations in the habitats of Z. *vivipara* in Latvia can be expected.

Natrix natrix in the Eastern European boreo-nemoral zone is considered to inhabit diverse forests, where moist deciduous stands being more typical for the species (Gruoudis 1987; Pikulik *et al.* 1988; Bondarenko & Starkov 1989; Dunajev & Haritonov 1989). As to *N. natrix* in the study area, the canopy composition was not correlated with the snake distribution. The species has a great dispersal ability and a large home range (Madsen 1984; Spellerberg 1988; Zuiderwijk *et al.* 1998b), resulting in a wide habitat niche breadth. However, some canopy features have been observed to be important. In my study, deciduous tree stands younger than 45 years were avoided (Figure 9). Deciduous trees (*Betula spp., Populus tremula, Alnus incana*) rapidly regenerate on clearings and fallow-lands, and in Latvia, unlike coniferous stands, deciduous stands have seldom been artificially planted and thinned (Brice 1998). Hence, the surface in young deciduous stands is shaded. In mature deciduous stands, surface is better exposed to light due to natural gap disturbance (Priedītis 1999).

In *N. natrix* clear preferences were observed for two drained forest types (Callunosa turf. mel., Vacciniosa turf. mel.), typical for old saturated peat mines. However, transect length in these types was insufficient for firm conclusions. Concerning forest types with transect lengths of more than 10 km, the *N. natrix* data showed positive preference values only for two more types (a wet type and a drained type). In the study area these latter two types were associated with a high density of amphibians (mainly *Rana temporaria*) (personal observation), which are a main food resource for *N. natrix* (Drobenkov 1995; Gregory & Isaac 2004). Amphibian density (i.e. prey availability) is certainly among the important factors determining the distribution of *N. natrix* in forest habitats. However, high amphibian density itself did not necessary result in the presence of *N. natrix* (personal observation).

Vipera berus, which was expected to be common in forests and bogs (see e.g. Viitanen 1967; Belova 1976; Gruodis 1987; Ognev & Laptikov 1989), was rarely encountered in both of the study areas. This probably reflects regional differences in the distribution of this species, as *V. berus* is frequent in forests - at least in some areas of Latvia (personal observation).

Lacerta agilis was also a rare species in forest habitats in both study areas. Several records were made in dry pine forest types where *Calluna vulgaris, Vaccinium* species, and grasses are dominant in the herb layer. Stands with similar herb layer composition are typical for this species in temperate Western Europe (Dent & Spellerberg 1987; Spellerberg 1988; Stumpel 1988; Glandt 1991), although the canopy can be dominated by different species. In other areas of sub-boreal Eastern Europe *L. agilis* also inhabits mainly dry pine (*Pinus sylvestris*) stands (Gruodis 1987; Pikulik *et. al.* 1988; Voitehov *et al.* 1989).

Use of Levins's index caused some counterproductive results when applied to habitat niche surveys. In KNP, it produced higher values for *N.natrix* than for *Z.vivipara* although the observed distribution of latter came closer to what was to be expected for species with wide niche breadth. In Levin's formula, maximum value of the niche breadth is attained when all types are exploited at equal proportions. However, censuses were not carried out at equal proportions in all forest types. When Levin's formula was applied to the proportions of transects in the various forest types, it resulted in values of 7.5 in KNP and 3.3 in GNP (42 and 30 % of the maximum, respectively). In two cases (*N. natrix* in KNP, and *Z. vivipara* in GNP) Levins's index for species was higher than this value. In both cases it simply indicated that the common forest types were not the most preferred. Another discrepancy was observed regarding differences between both National Parks. Index values were higher in KNP, although the coherence between the proportions of records and transect lengths was less marked than in GNP. Therefore, the application of Levins's index cannot be recommended for habitat surveys with unequal transect lengths in the various habitats.

Studies on the forestry impact on reptiles are relatively rare and deal mostly with the effect of tree logging in the tropical forests (e.g. Kutt 1993; Sartorius *et al.* 1999; Lima *et al.* 2001). The forestry impact in the temperate Europe is largely overlooked. Some information has been collected during inventories and surveys on reptile ecology in clearings and young stands (e.g. Boshansky & Pishchelev 1978; Stumpel 1987; Spellerberg 1988). However, the effect of forest drainage on reptiles remains obscure.

In the present survey, reptile niches overlapped mostly in drained forests. These forests are favored by both dry forest species (*A. fragilis*) and species that prefer wet forest (*Z. vivipara, N. natrix*), which is possible due to:
i) intermediate moisture conditions; draining seldom is complete, and some extra moisture usually persists in the soil, making the habitat suitable for both dry and wet habitat species;
ii) stabile water regime in habitat due to drainage ditches; under natural conditions, in raised bogs and wet forests large areas can be homogeneous dry or wet depending on the season. This could have a negative effect on reptiles, especially on species with limited dispersal ability;
iii) impact of drainage ditches on habitat structure; the increase of habitat diversity due to the presence of suitable basking places, shrubs and grasses on the banks, and the presence of permanent water supply essential for many animal species.

Of course, the conclusions drawn from a survey in one country cannot be extrapolated to the whole region of the temperate European forests. The study area (Latvia) is located in the middle of sub-boreal forest zone (Stanners & Bourdeau 1994). Sub-boreal forests form a belt between boreal and nemoral forests, which gradually narrows from Scandinavian Peninsula and Eastern Baltic to Western Siberia.

Therefore, the present data can be regarded representative for the forests of Baltic States, most of Belarus, and parts of Western Russia.

4. VEGETATION STRUCTURE AND COMPOSITION IN TERRESTRIAL REPTILE HABITATS IN LATVIA

4.1.Introduction

The spatial distribution of reptiles in habitats of the temperate climate zone is very uneven. In the majority of habitats only some specific microhabitats are actually used by reptiles, and these microhabitats often are not typical for the given habitat in general. Thus, lacertids may have been virtually absent from forest habitats in Europe before the onset of human economic activity and the creation of disturbed sites (Strijbosch 1999). This point of view, however, strongly oversimplifies the situation. In a closed forest habitat, suitable microhabitats develop under wind-created canopy gaps (Greenberg 2001). In addition, several species (including lacertid *Zootoca vivipara*) are also frequent in natural, undisturbed habitats, such as open stunted pine stands on the periphery of raised bogs (Boshansky & Pishchelev 1978; Zamolodchikov & Avilova 1989).

Although temperate reptile habitats generally have been described in many faunistic studies, few surveys on microhabitats with detailed vegetation analysis exist. Relatively well-studied is the Sand Lizard - *Lacerta agilis*, with relevant surveys carried out in Spain (Amat *et al.* 2003), Great Britain (House & Spellerberg 1983; Dent & Spellerberg 1987), Germany (Glandt 1991), Netherlands (Stumpel 1988), Sweden (Berglind 2000) etc. Less studied are the Common Lizard - *Zootoca vivipara* (Dent & Spellerberg 1987; Strijbosch 1988; Glandt 1991; Zamolodchikov & Avilova 1989), and the Slow Worm (e.g. Stumpel 1985). Some information on microhabitats of snakes in temperate Europe is presented in wider surveys (Viitenen 1967; Prest 1971; Madsen 1984). However, all of the studies mentioned above have at least one of the following shortcomings: i) the survey is limited to only one or very few sites, ii) the survey does not include all potentially suitable habitats, and iii) the survey is limited to 1-2 species.

The knowledge on species microhabitat preferences has obvious practical application in species conservation efforts, particularly in establishment of protected areas. But, relevant data on reptiles for Latvia is lacking, and previous surveys have dealt with habitats in the broader sense (see Chapters 2 and 3) or gave brief faunistic information for only some territories (e.g. Barševskis *et. al.* 2002; Čeirāns 2002b, 2003). Some very useful information, however, can be borrowed from older not strictly scientific literature (e.g. Siliņš & Lamsters 1934).

This paper presents some results of a wide survey conducted to clarify factors determining the distribution and abundance of reptiles in Latvia. The effect of large-scale factors, such as climate and macro-habitats, is analyzed Chapter 2. Here I present the analysis of a small-scale factor – microhabitat, with a description of vegetation characteristics typical for five reptile species, that are more or less regularly found in Latvia. Only terrestrial microhabitats were surveyed, and aquatic or semi-aquatic (banks of waterbodies) microhabitats were omitted. Habitats of the Smooth Snake (*Coronella austriaca*) in Latvia (this species is very rare and was not found in the present survey) are described in Chapter 5.

4.2.Methods

Data were collected in 1999-2003 on transects that can be regarded as representative for whole territory of Latvia. Their total length was 689.3 km, sampling was randomly stratified. A more detailed description of transect selection principles and censuses is published in Chapter 2.2.2. In the present analysis, only data from period with fully developed vegetation (3rd decade of May – 1st decade of September) was used.

Vegetation was described in circular plots with the centres in point, where reptile specimens were first spotted. The radius was 1.5 m for the moss layer and herbs, 5.0 m for shrubs, and 10.0 m for trees. The total number plots were: 27 for *L. agilis*, 136 - for *Z. vivipara*, 57 – for *A. fragilis*, 28 – for *N. natrix*, and 32 – for *V. berus*. In many cases the plots had elongated or irregular shape, because parts with very different vegetation were excluded. In cases where an observation was made near the border between two very different microhabitats (e.g. on forest edges) only one was regarded as a reptile habitat. A modified Braun-Blanquet method was used. Vegetation data was described as coverage according to the following coverage classes given in Table 11. The coverage was described separately for different height classes, taxons and ecological groups (see 4.2.).

Table 11

Vegetation cover values (mean ± SD) and weighted average for coverage in % on plots; unimportant factors are not included

Variable	*L. agilis*	*Z. vivipara*	*A. fragilis*	*N. natrix*	*V. berus*
Vegetation height layer					
≥ 10 m	0.0±0.0; 0	0.4±1.2; 5	1.4±2.0; 18	0.5±1.4; 7	0.2±0.8; 2
1.0-9.99 m	1.3±1.4; 9	1.7±2.0; 21	2.0±2.0; 25	2.4±2.1; 31	2.7±2.0; 32
0.99-0.5 m	1.1±1.1; 7	1.6±1.8; 17	1.2±1.8; 13	2.9±1.8; 35	2.3±1.8; 26
0.49-0.16 m	3.0±1.4; 31	3.1±1.4; 36	3.4±1.3; 40	3.0±1.7; 34	3.3±1.7; 44
≤ 0.15 m	1.5±1.5; 12	0.9±1.3; 7	0.9±1.5; 8	1.0±1.6; 11	0.5±1.0; 3
Mosses	1.1±1.1; 24	0.6±1.0; 16	1.3±1.4; 34	0.4±0.8; 12	0.3±0.8; 12
Wooded vegetation					
Pinus sylvestris	1.0±1.1; 6	0.5±1.1; 4	1.2±1.8; 14	0.5±1.1; 4	0.2±0.5; 1
Picea abies	0.1±0.6; 1	0.3±0.7; 2	0.6±1.3; 10	0.1±0.4; 1	0.7±1.4; 7
Betula	0.4±0.9; 3	0.6±1.2; 5	0.8±1.1; 5	1.3±1.8; 15	1.2±1.5; 11
Salix	0.2±0.5; 1	0.8±1.5; 9	0.9±1.6; 11	1.2±0.8; 13	1.3±1.7; 13
Juniperus communis	0.0±0.0; 0	0.0±0.0; 0	0.1±0.3; 1	0.0±0.0; 0	0.0±0.0; 0
Grasses					
Xeric grasses[a]	0.6±1.1; 4	0.1±0.5; 1	0.1±0.5; 1	0.0±0.0; 0	0.0±0.0; 0
Meso-xeric grasses[b]	0.7±1.2; 5	0.3±0.9; 2	0.5±1.2; 5	0.1±0.4; 1	0.1±0.4; 1
Mesic grasses[c]	0.8±1.2; 7	1.9±1.6; 16	1.5±1.6; 14	2.5±1.8; 26	1.7±1.5; 14
Calamagrostis	1.0±1.3; 7	1.1±1.6; 11	0.6±1.2; 5	0.9±1.5; 11	1.6±1.9; 19
Tall dune grases[d]	0.2±0.7; 1	0.0±0.0; 0	0.0±0.0; 0	0.0±0.0; 0	0.0±0.0; 0
Undershrubs					
Calluna vulgaris	1.2±1.7; 13	0.3±1.0; 3	0.4±1.1; 4	0.1±0.4; 1	0.2±0.6; 1
Vaccinium vitis-idaea	0.2±0.6; 1	0.2±0.7; 2	0.4±1.1; 4	0.1±0.4; 1	0.2±0.6; 1
Vaccinium myrtillus	0.0±0.0; 0	0.1±0.6; 1	0.7±1.4; 7	0.0±0.0; 0	0.2±0.6; 1
Other herbs					
Broadleaved (tall) herbs[e]	0.0±0.0; 0	0.7±1.2; 6	0.7±1.3; 6	1.1±1.5; 10	1.2±1.7; 13
Narrow-leaved (medium-size) herbs[f]	0.6±1.0; 4	0.3±0.7; 2	0.3±0.5; 1	0.3±0.5; 1	0.3±0.6; 1
Fabaceaceae (tall)[g]	0.3±0.5; 1	0.2±0.5; 1	0.1±0.4; 1	0.3±0.5; 1	0.3±0.6; 1
Melamphyrum	0.1±0.2; <0.1	0.2±0.6; 1	0.4±0.8; 2	0.1±0.6; 1	0.4±0.8; 2
Small "succulents"[h]	0.3±0.6; 1	0.0±0.0; 0	0.1±0.2; 1	0.0±0.0; 0	0.0±0.0; 0
Rumex (medium-size)	0.1±0.4; 1	0.1±0.2; <0.1	0.1±0.4; 1	0.0±0.0; 0	0.1±0.2; <0.1
Plantago	0.0±0.0; 0	0.1±0.2; 1	0.1±0.5; 1	0.1±0.2; <0.1	0.0±0.0; 0
Hypericum	0.0±0.0; 0	0.0±0.0; 0	0.1±0.4; 1	0.0±0.0; 0	0.0±0.0; 0
Moss layer					
Lichens on ground	0.8±1.5; 8	0.1±0.3; 1	0.2±0.7; 1	0.0±0.0; 0	0.0±0.0; 0
Sphagnum	0.0±0.0; 0	0.1±0.4; 1	0.0±0.0; 0	0.1±0.6; 1	0.0±0.0; 0

a – small, tufted grasses on infertile soils with all leaves thread-like (*Koeleria glauca, Nardus stricta, Festuca ovina* agg.); b – medium-sized loosely tufted or tufted grasses on xero-mesic soils with all or some leaves thread-like (*Deschampsia flexuosa, Festuca rubra*); c – mesic grasses with flat leaves (*Festuca pratensis, Poa pratensis, P. trivialis, Dactylis glomerata, Bromus arvensis* etc); d – tall dune grasses (*Leymus arenarius, Ammophila arenaria*); e – tall herbs with large, broad leaves (umbellifers – *Aegopodium podagraria, Angelica sylvestris, Daucus carota* etc; meadowsweet (*Filipendula ulmaria*), thistles (*Cirsium*), nettle (*Urtica dione*)); f – medium-size herbs with simple narrow to elliptical leaves from daisy (*Taraxacum, Crepis, Senecio, Centaurea, Hieracium* etc), bellflower (*Jasione Montana*), and teasel (*Knautia arvensis*) families; g – tall or climbing herbs from the pea family (*Viccia, Lathyrus, Astragalus, Melilotus*); h – small evergreens on bare places with succulent-like, fleshy leaves (*Sedum acre, Honkenya peploides*).

Vegetation cover scale as follows (except for mosses): 0-absent; 1-scanty (cover 1-5%); 2- rare (6-14%), 3-medium (15-33%), 4-common (34-67%), 5-abundant (>67%); the moss layer: 0-not developed (coverage <10%), 1- poor (10-32%), 2-medium (33-67%), 3- well developed (>67%).

To reduce misidentifications (many herbs could not be identified as they lacked flowers), and to reduce the number of accidental variables, taxons were pooled into ecological groups from taxons with similar size, habitus and ecology. These groups were arbitrary, selected on the basis of literature sources (Pētersone & Birkmane 1980, Fitter at al. 1984, Fitter et al. 1996) and personal experience. Exceptions were made for easily identifiable and frequent taxons (trees, undershrubs, some herbs), which were treated at the species level.

Microhabitat use among reptile species was examined using discriminant function analysis (DFA). Although the data did not meat the Box'M test of homogeneity of covariance matrices, this requirement is rarely met in ecological analysis, and DFA is robust enough to withstand some violation of homogeneity assumption (Tabachnik & Fidell 1996). The majority of the correlations between variables were well below 0.50, and all were included in analysis. Raw data were used because transformations produce biologically similar or identical results in DFA (McAlpine & Dilworth 1989). All statistics were conducted using the SPSS for Windows Version 11.5 (2002)® program package.

4.3.Results

Two discriminant functions derived from the analysis correctly classified 60.7 % of original cases (Table 12). The first dicriminant function (DF1) showed positive correlations with variables characterizing low vegetation (small "succulents" (mainly *Secum acre*), lichens on ground, small tufted grasses, and heath *Calluna vulgaris*), typical for very poor soils and relatively xeric conditions (Table 13). DF1 had negative correlations with variables characterizing generally moist (mesic) conditions: tall herbs with large, broad leaves (umbellifers - Apiaceae etc), mesic grasses (*Festuca, Poa, Dactylus glomerata* etc.), and some deciduous trees (*Salix, Betula*). Hence, this function discriminated species along a xeric – mesic vegetation gradient.

Table 12

Summary of DFA statistics

Statistic	**DF1**	**DF2**
Eigenvalue	0.771	0.518
% of variance	38.7	26.0
Wilks Lambda	0.204	0.361
Chi-Square	395.69	253.358
df	220	162
p	<0.001	<0.001

The second discriminant function (DF2) had positive correlation with variables characterizing *Myrtillosa* - type, and similar forests (Bušs 1997), belonging to *Vaccinio myrtilli-Pinetum* association (Priedītis 1999). Such forests are common in Latvia; they are dominated by pine (*Pinus sylvestris*) in canopy, with well-developed moss layer, and bilberry (*Vaccinium myrtillus*)-dominated herb layer. The positive correlations with St John's wort (*Hypericum*), plantain (*Plantago*), and sorrel (*Rumex*) were due to observations on forest paths as these species are typical for verges, and not for intact forest (Bušs 1997). DF2 had a negative correlation with small-reeds (*Calamagrostis*) and some other herb vegetation typical for disturbed sites, such as roadsides and clearings (Bušs 1997). Thus, this function discriminate reptiles along a disturbance gradient in upland pine forests.

Although habitats greatly overlapped (Figure 13), group centroids showed good separation among species (Table 14). *Lacerta agilis* prefers xeric sites (see centroid at DF1), while both snake species prefered sites with tall herb layer and shrubs. Two other lizard species had intermediate positions along this gradient. *Anguis fragilis* often were associated with relatively intact pine forest (centroid at DF2), while other reptiles with mainly disturbed sites with grass cover.

Table 13

DFA structure matrix

Variable	**DF 1**	**DF 2**
Small succulents	0.448*	0.004
Lichens on ground	0.402*	0.071
Xeric grasses	0.329*	-0.014
Calluna vulgaris	0.320*	0.001
Tall dune grases	0.277*	-0.056
Broadleaved (tall) herbs	-0.258*	-0.042
Mesic grasses	-0.236*	-0.082
Salix	-0.207*	0.006
Betula	-0.195*	-0.028
Meso-xeric grasses	0.191*	0.141
Low (≤ 0.15 m) vegetation	0.158*	-0.003
Narrow-leaved (medium) herbs	0.138*	-0.068
Vaccinium myrtillus	-0.054	0.457*
Trees ≥ 10 m	-0.099	0.438*
Moss layer	0.186	0.394*
Pinus sylvestris	0.161	0.310*
Hypericum	-0.012	0.279*
Tall (0.5-0.99 m) herbaceous vegetation	-0.230	-0.240*
Plantago	-0.032	0.237*
Juniperus communis	-0.010	0.222*
Calamagrostis	-0.029	-0.222*
Melamphyrum	-0.118	0.196*
Vaccinium vitis-idaea	-0.06	0.181*
Fabaceaceae (tall)	0.011	-0.125*
Rumex	0.106	0.123*

Variables with largest absolute correlation with given function marked with asterisk; only variables with correlation >0.1 are shown; for variable explanations see also Table 11

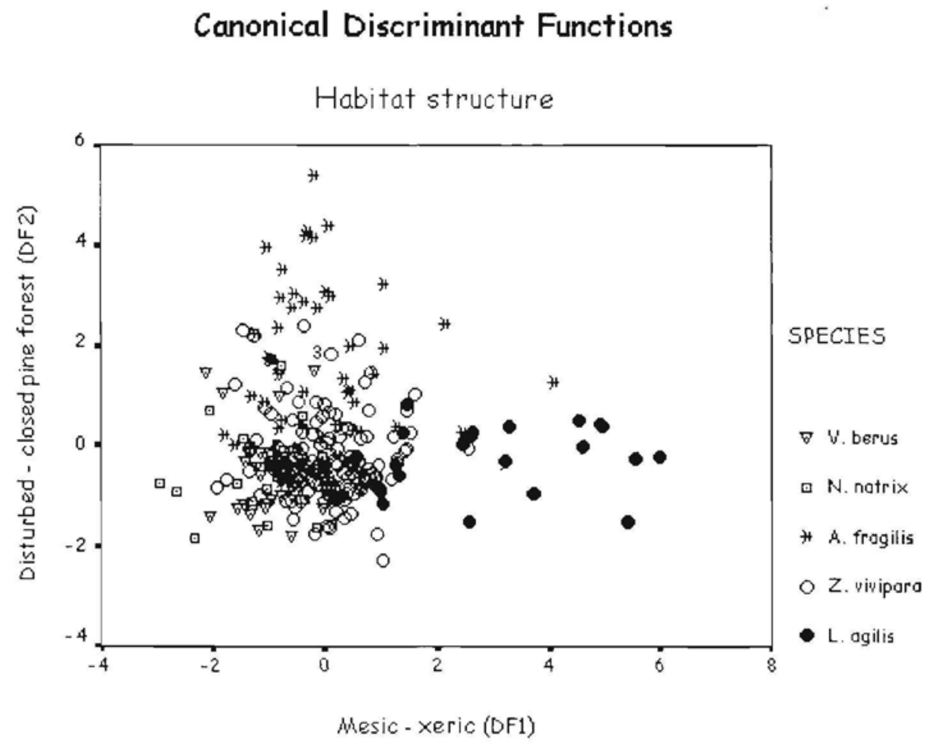
Table 14

Functions at group centroids

Species	**DF 1**	**DF 2**
Lacerta agilis	2.458	-0.337
Zootoca vivipara	-0.056	-0.296
Anguis fragilis	-0.091	1.401
Natrix natrix	-0.942	-0.531
Vipera berus	-0.852	-0.490

Figure 13

Discrimination among reptile species for microhabitat



4.4.Discussion

There is a considerable microhabitat overlap among reptiles in Latvia (Figure 13). Predominantly grassy medium-height vegetation with some wooded vegetation cover is typical for all species (Table 11).

The microhabitat niches of two species are very different from those occupied by the other species. The Sand Lizard (*L. agilis*), can occur on open, very xeric habitats with low succulent-like herbs (*Sedum acre*), low densely-tufted grasses, heath (*Calluna vulgaris*) and lichens. However, the normal microhabitat for *L. agilis* in Latvia is less xeric than the described above. It is most often found in sparse low pine (*Pinus sylvestris*) stands, with herb cover dominated by various grasses, and a relatively large proportion of heath. *Lacerta agilis* avoids sites with tall broad-leaved herbs, although some ferns (e.g. *Pteridium aquillinum*) may be present (Dent & Spellerberg 1987). These habitats are generally similar to *L.agilis* habitats in Western Europe (House &

Spellerberg 1983, Strijbosch 1986, Dent & Spellerberg 1987, Stumpel 1988, Glandt 1991), but there are some differences in ground cover – e.g. *Erica* undershrubs are naturally absent in Latvia, and the grass cover can have a different taxonomic composition.

The other species with a very distinctive microhabitat niche is the Slow Worm (*A .fragilis*). It is the only species found in virtually intact forest: dry or drained pine-dominated forests, where undershrubs (mainly Bilberry - *Vaccinium myrtillus*) dominate the ground cover. The moss cover is composed of a thick but loose feather moss (*Pleurozium*, *Hylocomium*) mat, which creates good hiding places for this secretive species. In most cases observations in such forests were made on paths, near canopy gaps or close to the forest edge. However, in some cases there were no open sites nearby. The canopy in these forests is relatively diffuse, and the ground cover apparently receives sufficient heat for this species. The importance of these forests as *A.fragilis* habitats is confirmed by previous studies (Čeirāns 2002a, 2004), although their ecotops and borders with other habitats are still more important than the intact forest (Stumpel 1985).

DF centroids for both snake species were very close, indicating similar microhabitat composition preferences. Both prefer sites with some (~10-40%) shrub (*Betula, Salix*) coverage and tall grass vegetation. Characteristic also is the presence of tall herbs with broad leaves, e.g. umbellifers. Such vegetation offers good shelter and supports small prey vertebrates, although the presence of more open basking places may also be a requirement. The above characteristics describe the summer habitat for *N. natrix* and *V. berus*, which may use different habitats for wintering, mating, and feeding (Viitanen 1967; Prest 1971; Madsen 1984).

The lack of discrimination along a mire function was unexpected, the reptile species generally avoid (*L. agilis, A. fragilis*) or are frequent (*Z. vivipara,* both snake species) in such habitats (Viitanen 1967, Belova, 1976, Zamolodchikov & Avilova 1989). This may be explained by undersampling of microhabitats with distinct mire vegetation, characterized by Cotton-grass (*Eriophorum vaginatum*), Northern Bilbery (*Vaccinium uliginosum*), Labrador Tea (*Ledum palustre*), Bog Rosemary (*Andromeda polifolia*) etc., since transects were located mostly along paths, cuttings and other sites with disturbed vegetation. Or, these microhabitats may be less important for reptiles than disturbed sites (Boshansky & Pishchelev 1978, Čeirāns 2004) where the typical mire vegetation is degraded or disappeared. We did not find any association with some other wetland vegetation (e.g. Purple Moor-grass *Molinia coerulea*) in Latvia, as has been described in Western Europe (Dent & Spellerberg 1987; Strijbosch 1988).

Site occupancy by reptiles, of course, is not only the consequence of microhabitat characteristics, but also many other factors, such as site exposure, spatial heterogeneity of environment, the presence of water bodies, more open or more closed microhabitats in vicinity, shelters, prey availability etc. However, the present work showed differences in vegetation structure and composition among reptile microhabitats, indicating the relative role of disturbance for various species in some forest habitats. The observations made were useful identifying the microhabitat characteristics typical for these species in Latvia.

5. DISTRIBUTION AND ECOLOGY OF THE SMOOTH SNAKE (*CORONELLA AUSTRIACA*) IN LATVIA

5.1.Introduction

The smooth snake (*Coronella austriaca*) is an ovo-viviparous species up to 80 cm in total body length, ranging from Spain to north-western Iran and Trans-Ural Russia (Arnold 2002). Latvia is located on the northern periphery of the range, and the species is absent in Estonia; *Coronella austriaca* is very rare and considered as endangered in Latvia (Ingelög *et al.* 1993).

The previously published data on *C. austriaca* in Latvia are very fragmentary, and deal mostly with its distribution (Siliņš & Lamsters 1934; Spuris *et al.* 1974; Lipsbergs *et al.* 1990). The records also include observations of naturalists not familiar with herpetology, who may mistake *C. austriaca* for some other species (*Anguis fragilis* or *Vipera berus*). In the second half of the 20th century, only few finds were recorded, indicating that the species has probably disappeared in several localities. There are no recent finds near the city of Rīga where the species was regularly found (Siliņš & Lamsters 1934) in the first half of the century. The study of *C. austriaca* is hindered by its secretive habits (Spellerberg & Phelps 1977; Larsson 1995).

The aim of the present survey was to summarise the existing data on *C. austriaca* in Latvia, to verify the data on dubious *C. austriaca* records, and to collect data on habitats and ecology of local populations.

5.2.Materials and methods

Data on the distribution of *C. austriaca* in Latvia in the first half of the 20th century were borrowed from (Ecke 1927; Grosse & Transehe 1929; Siliņš & Lamsters 1934), older data were omitted in the present paper. Data on the distribution of *C. austriaca* in Latvia in the second half of the 20th century were obtained from published and unpublished reports (Ļuta 1973; Spuris *et al.* 1974; Zirnis 1980; Lipsbergs *et al.* 1990; Pupiņš & Škute 1992). The plausibility of the latter data was assessed and new information on distribution was acquired from personal communications with the persons who made these observations or (and) published this information. The exact locations of the finds before 1980s, however, remain unknown.

Field observations and descriptions of habitats were made in 1994-1997 in six verified locations where the smooth snake had been found in the late 1980s and in the 1990s by other observers: one location in the Šlītere National Park and five locations in the Ķemeri National Park. Locations in the latter were visited 2-4 times each in June-August 1996, excepting one location near Kūdra, which was visited 19 times in 1994-2003. The location in the Šlītere National Park was visited 4 times in June-July 1996.

Every location was thoroughly searched in optimal weather conditions (warm, but not hot, mostly in morning hours) for 1-3 hours, depending on the size of habitat, and included search under potential hiding places. Other reptile species were also recorded. In some cases, they were counted on 1.5-3 km long and 3 m wide transects. Verified data gathered by other observers were also used for evaluation of the spatial distribution of the species. Data on the number and size of juveniles were obtained from females (n=3) caught in the field whilst pregnant and examined after parturition in the Laboratory of Ecology, Rīga Zoo.

5.3.Results

5.3.1.Distribution

In the 19th century and in the 1st half of the 20th century, *C. austriaca* was often found in the Coastal Lowland south of the Gulf of Rīga between Langaciems (present-day Trīsciems) and Ķemeri (in Daugavgrīva, Piņķi, Beberbeķi, Kauguri, etc.) where the species has apparently disappeared; it was also found in few other locations in western and central Latvia (Kolka, Roja, Ropaži); Rucava and Kandava in western Latvia were also noted as possible locations (Ecke 1927; Grosse & Transehe 1929; Siliņš & Lamsters 1934) (Figure 14).

Table 15

Published and new records of *Coronella austriaca* in Latvia in the second half of the 20th century

Reference	Location	Year of observation	Comments
Ļuta 1973	Mērsrags (western Latvia)	Early 1970s	The correct description of the species is given
Spuris *et al.* 1974	Surroundings of Jaunjelgava, Dobele District (both in southern Latvia), and Valka District (northern Latvia)	1946...1973	Observations were made by naturalists, no exact localities were mentioned; these observations could be considered as doubtful
Zirnis 1980	Near Ķemeri, Sloka, Melluži (all in central Latvia), near Cēsis, two locations in Limbaži District, Oleri (all in northern Latvia)	1954...1980	Records from Cēsis (V. Pilāts, pers.comm..) and Limbaži District (A.Bērziņš pers.comm..) are incorrect; the remaining location mentioned for northern Latvia, Oleri, should be considered as doubtful because located close to Estonia where the species is absent (Ingelög *et.al.* 1993)
Lipsbergs *et.al.* 1990	Near the eastern shore of Lake Engures at Bērzciems, vicinity of Lake Usmas (both in western Latvia)	The 1970s	The former record was verified latter by zoologist M. Šternbergs (pers.comm..); the latter has not been verified (J.Lipsbergs, pers.comm..)
Pupiņš & Škute 1992	Ilgas (southeastern Latvia)	Early 1990s	This record about a possible find was a mistake (M.Pupiņš, pers.comm..)
Unpublished	Five locations in the Ķemeri National Park (central Latvia)	1979...2003	Data collected by A.Poikans, verified by personal communication and observations by the author
Unpublished	Near Roja (western Latvia)	1986...1988	Personal communication by N.Savenkovs, verified by the correct description
Unpublished	Western Side of the Bažu Bog in the Šlītere National Park (western Latvia)	1993...2004	Observations by the author, the students, and staff of the Faculty of Biology, University of Latvia

Data no records of *C. austriaca* in Latvia in the second half of 20th century, which better reflect the present distribution, are summarised in Table 15. Verified location of the species appear to be confined to the Coastal lowland from the Šlītere National Park to the Ķemeri National Park (Figure 14). In the 1990s and early 2000s, *C. austriaca* known populations were located only in the Šlītere National Park and the Ķemeri National Park.

5.3.2.Populations

The Šlītere National Park (SNP). *Coronella austriaca* was found only in one location on 3 km long and up to 5 m high old dune ridge on the north-western side of the Bažu bog. Suitable habitats (open and dry low pine stands) are fragmentary on the top and the south-eastern slope of the ridge. Human impact here is insignificant. The population has survived regardless of vegetation destruction by the 1992 forest fire. I visited the site 4 times in 1996, but observed the snake only once. However, the species was regularly found in 1993-2004 by lecturers and students in field courses of the Faculty of Biology, University of Latvia, and their descriptions can be considered as valid records.

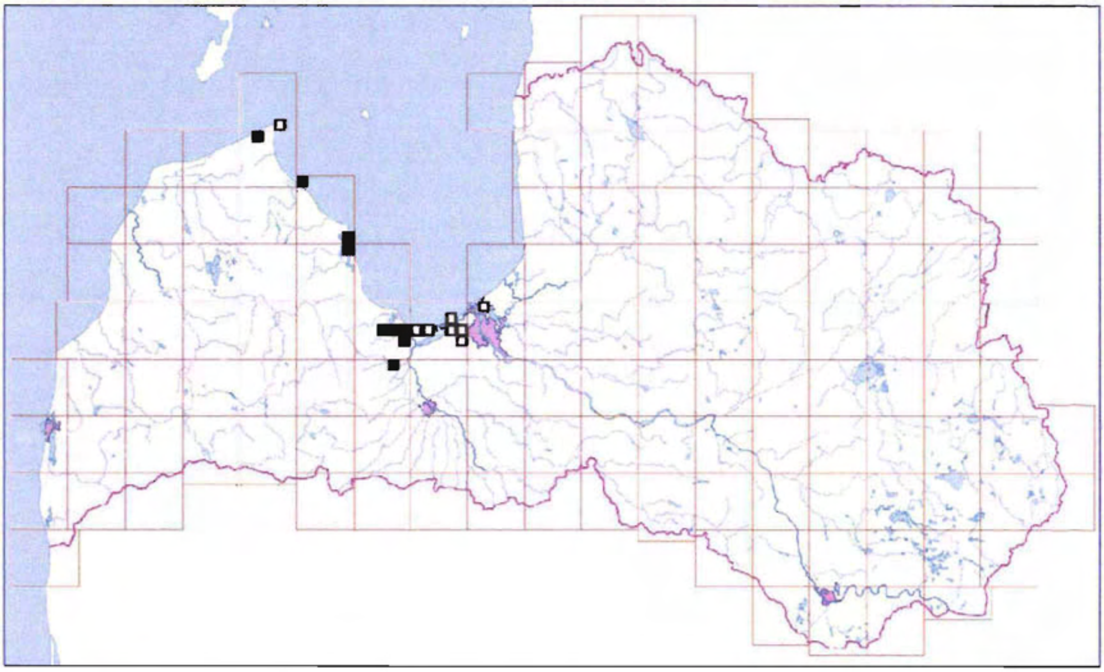


Figure 14

Valid records of *Coronella austriaca* in Latvia after World War II (solid squares), supplemented by the records from the first half of the 20th century (open squares)

The Ķemeri National Park (KNP). *Coronella austriaca* was regularly found in the last two decades by various observers only in one location (near Kūdra). The total area of this site, including wet forest on peat, drained forest surrounding old peat mines, and the bog, is about 40 ha. *Coronella austriaca* was observed only on a road embankment within a 1 km interval. The population appears to have declined. In 1982-1984, 1 to 6 specimens per 0.5-1 hour visit were regularly observed, but latter their numbers diminished (A.Poikāns, pers.comm.). In 1994-2003, I observed the snake here only 5 times during 19 visits (1-3 specimens per visit). In two cases snakes were dead. The area is often visited by the locals. A possible reason for the population decline, however, is a change of water regime by amelioration causing overgrowth with birch in a wide surrounding area, including the embankment. In four other locations of KNP, only single specimens were found in 1976-1992, with one exception where it was observed several times on the early 1980s (A.Poikans, pers.comm.). No snakes were found there during the examination of these localities by the author in 1994-1996. In early 2000s, *C. austriaca* was observed in two more locations in southern and eastern parts of KNP (V.Vintulis, pers.comm.).

5.3.3.Habitats

Observed habitats of *C. autriaca* are the following:

1) **Open dry stands on sand.** The tree stands are low, 1-9 m (usually 2-5 m) high, sparse (coverage 10-50 %) and consist of pine (*Pinus sylvestris*) and birch (*Betula pendula, B. pubescens*). In the herb layer, dominant species are heath (*Calluna vulgaris*) and grasses (mostly *Lolium perenne, Festuca* agg. *ovina, Deschampsia flexuosa,* and *Calamagrostis epigeios*. Such habitat was found on:
1a) old dunes beside bogs, where the herb layer is dominated by *Calluna vulgaris* (coverage 60-80 %), with cowberry (*Vaccinium vitis-idea*), mosses (*Polytrichum juniperinum, Pholia nutans*) and lichens (*Cladina rangiferina*); on southern slopes and paths, favoured by the snake, there are also some grass (*Festuca* agg. *ovina, Calamagrostis epigeious*) cover (coverage usually less than 20%); common herb species are *Chamaenerion angustifolium, Hieracium pilosella, Rumex acetosella* (1 site in SNP, 2 - in KNP);
1b) clearings in dry pine forest of Cladinoso-callunosa and Vacciniosa (Bušs1997) types, where the herb layer is generally similar, but dominated by grasses (coverage 20-60%), occasionally by heath (2 sites in KNP);

2) **Open pine stands on peat.** The snake in the habitat was found only on low, dry and grassy embankment with a wide path on the top. The path was bordered by scattered low (1-2 m), but dense willow (*Salix cinerea, S. myrsinifolia*). The herb layer here is dense (coverage up to 80%), consisted mostly of *Carex rostrata, C. oederi* and *Calamagrostis arundinacea*. The forest on peat itself was partially drained, located around old flooded peat mines, and formed by sparse pine and birch stands. The herb and moss layer here consisted of *Calluna vulgaris, Eriophorum*

vaginatum, Ledum palustre, Sphagnum magellanicum, S. compactum, and *Polytrichum commune* (1 site in KNP).

5.3.4. Notes on biology

In the current investigation, *C. austriaca* was observed in both fine and cloudy weather, usually at 20-27 °C. In spring, the earliest observation was made on April 22 in KNP. In captivity, the observed fecundity was low, with 4-6 juveniles being born in the second half of August. The size of juveniles (n=13) was: body length 131-159 (149.9±2.1) mm, caudal length 23-30 (27.6±0.6) mm, and weight 1.46-2.49 (2.16±0.07) g. After birth, 2-4 unfertilised eggs were also found.

In five of six *C. austriaca* locations visited, the Sand Lizard (*Lacerta agilis*) was also found. Both species inhabited the old dunes on bog sides and clearings in dry pine forest. The density of *L. agilis* there was low, as 1-3 specimens were encountered in each area in each visit. The location near the Kūdra peat bogs supports a different herpetofauna. Four other reptile species were found: the Viviparous Lizard (*Zootoca vivipara*), the Slow Worm (*Angius fragilis*), the Grass Snake (*Natrix natrix*), and the Adder (*Vipera berus*). The mean density of *Z. vivipara* that was counted on the grassy embankment was only 7-8 (maximum 25) individuals/ha. The density of *Z. vivipara* in the drained pine-birch forest (Callunosa turf.mel.) was lower, but in the forest on wet peat (Sphagnosa), only 1-2 specimens on the banks of small lakes were found. *Anguis fragilis* was observed regularly on the embankment and in the drained forest. In the wet forest it was very rarely observed, and was found only near the lakes. The observation frequency ratio for *N. natrix, C. austriaca* and *V. berus* was 8 : 2 : 1. *Natrix natrix* was widely distributed along the embankment and the old peat mines. *Vipera berus* was found in the drained forest with well-developed tree cover, while *C. austriaca* preferred a quite open site on the embankment. All of the snake species probably used a common wintering place under concrete blocks in the southern part of the area, where all species were observed.

5.4.Discussion

The verification of records of *C. austriaca* proved that some of these finds actually belonged to *A. fragilis* or *V. berus*, or (and) the exact location of the find presently is unknown. New records of this rare species should be verified before publishing by persons familiar with herpetology, and the exact locations should be mentioned. However, publication of a detailed map of the location is not recommended to avoid undesirable disturbance by tourists or animal collectors.

Coronella austriaca in Latvia so far is found only in the comparatively narrow coastal zone of the Gulf of Rīga in western Latvia. The population in Latvia is apparently isolated from the nearest populations that inhabit southeastern Lithuania (Gruodis 1987), and central Belarus (Pikulik *et al.* 1988). The species prefers rocky habitats in the southwestern Sweden, where stones are important retreat sites (Larsson 1995). In contrast, populations in Latvia are found mostly on sandy habitats, as rocky soils are not characteristic for the species area in Latvia.

Coronella austriaca in Latvia is located on the northern periphery of the distribution range. The main distribution-limiting factor in Latvia could be the climate. Four of the six locations studied are situated near or on sides on bogs, where the summer temperatures in large areas may be considerably higher than in the surroundings. Constantly dry or drained sites such as old dunes and embankments adds structural diversity in these very uniform, wet areas, and offer suitable wintering sites. The presence of *C. austriaca* mostly in such sites may indicate that the summer microclimate is very important limiting factor. On the other hand, so far species has been found only in the Coastal Lowland of western Latvia characterized by the mildest winters in Latvia. Hence, the combination of both climate factors could be important.

There is some controversy regarding feeding of *C. austriaca*. In Belarus, snake's diet consists mainly of reptiles, particularly *Z. vivipara* (Drobenkov 1995). Rodents, especially nestling juveniles, may also constitute the main part of the snake's diet (Spellerberg & Phelps 1977). The density of reptiles in *C. austriaca* locations in Latvia appears to be low. However, two of three adult specimens of *C. austriaca* caught in KNP ate only lizards in captivity, and only one consumed newborn mice, suggesting a preference also for lizards in the field situation.

Specimens of *C. austriaca* were found yearly almost in the same place within a distance of some dozen metres. The snake is sensitive to habitat destruction as the dispersal ability of the species is limited (Spellerberg 1986). The area of each of the suitable habitats in Latvia is only 1-3 ha, corresponding to the estimated individual activity range of 1.7-3.3 ha in Sweden (Larsson 1995). In England the local populations of *C. austriaca* are small (~15-35 individuals) (Spellerberg & Phelps 1977). The above indicates a great risk of accidental loss of the local populations.

Long reproductive cycle (one birth event in two years) (Gooddart & Spellerberg 1980), low fecundity, specific feeding requirements, and the small number of snakes in potential donor populations from Latvia makes this species unsuitable for the captivity breeding programs with following re-introduction or population re-inforcement. Therefore, the conservation actions on *C. austriaca* in Latvia should be focused on:

i) search for new populations, particularly in the relatively untouched areas of Coastal Lowland between Kolka and Ventspils; establishing of microreserves there;

ii) monitoring of known populations; maintenance of vegetation in the pre-canopy closure stage of succession, by thinning if necessary; creating a patches of open low pine, pine – birch stands with patchy but dense grass and heath cover in suitable sites;

iii) continuation of research on the snake's ecology, and localization of the priority conservation sites (wintering dens, preferred microhabitats, feeding grounds, etc.) in known populations.

6.MAIN CONCLUSIONS

The distribution and abundance of reptiles in Latvia is determined mostly by habitat and climate factors, while anthropogenic factors have a mainly local effect on most of the species. However, the latter still can be decisive in some areas (Zemgale Plain) or species (proportion of agricultural lands in *Anguis fragilis*).

The Sand Lizard (*Lacerta aglis*) is a rare species in Latvia; it prefers relatively xeric sites with sparse low pine stands, where the herb cover dominated by grasses, heath, and also small "succulents" (*Sedum acre*) and lichens. The species is more abundant in areas with a hot summer climate, and a high proportion of various dry pine forests.

The Common Lizard (*Zootoca vivipara*) is the most abundant and widespread reptile species in Latvia, inhabiting diverse habitats. In its typical microhabitat vegetation is grassy, medium-height, and with some wooded vegetation cover. *Zootoca vivipara* is more abundant in forested areas, where it prefers wet or drained forest types with considerable proportion of pine in canopy. The species is more numerous in areas with relatively cool summers, although this factor is less important than habitat.

The Slow Worm (*Anguis fragilis*) is the second most common reptile species. Habitat is the decisive factor for the spatial distribution of populations of this species. *Anguis fragilis* is rare in regions with a high proportion of agricultural lands, and is more often found in forested areas. The most suitable are dry or drained pine forests, and wet stands are avoided. *Anguis fragilis* also inhabits (pine) stands with closed canopy that is not characteristic for any other reptile species in Latvia.

The Smooth Snake (*Coronella austriaca*) is very rare in Latvia, and all the valid records of this species in the 2nd half of the 20th century are confined to the Coastal Lowland of western Latvia. Till the 1st half of the 20th century the species was also found in the surroundings of Riga both sides of the River Daugava, where it has disappeared. Typical habitats are sparse and dry stands of low pine and birch where the ground cover is dominated by heath and grasses. *Coronella austriaca* is found also on the periphery of raised bogs – on dry hills or in drained places.

The regional abundances of the grass snake (*Natrix natrix*) and the adder (*Vipera berus*) in Latvia are determined mostly by the climate factor. *Natrix natrix* is common only in lowlands, where winters are milder, but *Vipara berus* – in the regions with harsher winters. The mechanism why the winter factor has opposite effect on both species, is unclear. Probably in *Vipera berus* it is related with the selection of the collective wintering dens in the sites with southern exposure, where they are adversely affected by the thaws with following frosts.

Typical summer microhabitats of both species above are characterized by the presence of more or less developed shrub layer, and tall grasses in the herb layer, often with the high coverage of broad-leaved herbs (umbellifers etc.).

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REFERENCES

1. Amat F., Llorente G.A. & Carretero M.A. 2003. A preliminary study on thermal ecology, activity times and microhabitat use of Lacerta agilis (Squamata: Lacertidae) in the Pyrenees. *Folia Zool.* 52 (4): 413-422
2. Anonymous 2003. *Overview of the Latvian indicators of sustainable development.* Latvian Environment Agency, Rīga. [In Latvian]
3. Arnold N.E. 2002. *Reptiles and amphibians of Europe. 2nd edition.* Princeton University Press.
4. Avis P.G. 1997. The forest typology in Latvia: an overview and comparison. *Proceedings of the Latvian Academy of Sciences. Section B* 51 (5/6): 195-199.
5. Barševskis A., Savenkovs N., Evarts-Bunders P., Daniele I., Pētersons G., Pilāts V., Zviedre E., Pilāte D., Kalniņš M., Vilks K. & Poppels A. 2002. *Fauna, flora and vegetation of Silene nature Park.* Baltic Institute of Coleopterology, Daugavpils.
6. Belova Z.V. 1976. Spatial structure of the population of adder (Vipera berus). *Ekologija* **7:** 71-75 [In Russian].
7. Berglind S.-A. 2000. Demography and management of relict sand lizard *Lacerta agilis* populations on the edge of extinction. *Ecol. Bull.* **48:** 123-142.
8. Berkgaute R., Gailitis A. & Katelo I. 1999. *Latvian state of environment report '97.* Environmental consulting and monitoring centre, Rīga.
9. Blouin-Demers G. & Weatherhead P.J. 2001. Habitat use by black rat snakes (Elaphe obsoleta obsoleta) in fragmented forests. *Ecology* **82:** 2882-2896.
10. Bondarenko D.A. & Starkov V.G. 1989. About ecology and distribution of the Grass Snake, Natrix natrix, in the territory of Moscow City, and in the south of the Moscow District. In: *Amphibians and reptiles of the Moscow Region.* Nauka Publishers, Moscow [In Russian].
11. Boshansky A.T. & Pishchelev V.A. 1978. Effect of some forms of economical activity on distribution and numbers of Vipera berus. *Zool. Zh.* **57**: 1695-1698. [In Russian with English abstract].
12. Brice S. (ed.) 1998. *Handbook of forest.* State Forest Service, Riga. [In Latvian].
13. Broks J. (ed.). 2003. *The encyclopedia of forest. Volume 1.* Apgads Zelta Grauds Publishers, Rīga. [In Latvian].

14. Brūmelis G., Lapiņa L., Nikodemus O. & Tabors G. 2000. Use of artificial model of monitoring data to aid interpretation of principal component analysis. *Environ. Modell. Softw.* **15**: 755-763.
15. Bušs K. 1997. Forest ecosystem classification in Latvia. *Proceedings of the Latvian Academy of Sciences. Section B* 51 (5/6): 204-217.
16. Costanzo J.P. 1989. Effects of humidity, temperature, and submergence behavior on survivorship and energy use in hibernating garter snake, Thamnophis sirtalis. *Can. J. Zool.* **67**: 2486-2492.
17. Čeirāns A. 2000. The smooth snake (Coronella austriaca Laur.) in Latvia: distribution, habitats, and conservation. *Proceedings of the Latvian Academy of Sciences. Section B.* **54:** 85-90.
18. Čeirāns A. 2002*a*. On the importance of tree stand composition and age in forest habitats of Anguis fragilis, Zootoca vivipara, and Natrix natrix. *Herpetozoa* **15:** 63-74.
19. Čeirāns A. 2002*b*. Reptiles and amphibians of the Gauja National park, Latvia. *Biota* **3:** 17-26.
20. Čeirāns A. 2003. Reptiles and anurans of the Kemeri National Park, Latvia. In: *Biodiversity and conservation of boreal nature: proceedings of the 10 years anniversary symposium of the nature Reserve Friendship* (Heikkila R. & Lindholm T. (eds.)). The Finnish Environment 485, Kainuu Regional Environment Centre.
21. Čeirāns A. 2004. Reptiles in sub-boreal forests of Eastern Europe: patterns of forest type preferences and habitat use in Anguis fragilis, Zootoca vivipara and Natrix natrix. *Herpetozoa* **17**: 65-74.
22. Čeirāns A. In press. Reptile abundance in temperate-zone Europe: effect of regional climate and habitat factors in Latvia. *Russian Journal of Herpetology.*
23. Dent S., Spellerberg I.F. 1987. Habitats of the lizards Lacerta agilis and Lacerta vivipara on forest ride verges in Britain. *Biological Conservation* **42**: 273-286.
24. Drobenkov S.M. 1995. Comparative analysis of diet in sympatric snakes Vipera berus (L.), Natrix natrix (L.), Coronella austriaca (Laur.). *Ekologija*, 1995 (3): 222-226 [In Russian].

25. Drümpelman E.W. & Friebe W.C. 1806. Getreue abbildungen und naturhistorische beschreibungen des thierreichs aus den nördlichen prowinzen Russlands, vorzüglich Liefland, Estland un Kurland. Hf. 1. Riga.
26. Dunajev J.A., Haritonov N.P. 1989. Ecological notes on amphibian and reptile fauna of the Moscow District. In: *Amphibians and reptiles of the Moscow Region.* 'Nauka' Publishers, Moscow [In Russian].
27. Ecke H. 1927. Die Glattnater (Coronella austriaca (Laur.)) in den Ostsee-provinzen. *Korrespondenzblatt des Naturforscher-Vereins zu Riga,* 59: 21.
28. Fammler, H., Veidemane, K., Ruskule, A., Simanovska, J., Indriksone, D. & Kipper, K. (2000). *2nd Baltic state of the environment report based on environmental indicators.* Baltic Environmental Forum, Riga.
29. Fitter R., Fitter A. & Blamey M. 1996. Wild flowers of Britain et Northern Europe, 5th edition. Harper Collins Publishers.
30. Fitter R., Fitter A. & Farrer A. 1984. Collins guide to the grasses, sedges, rushes and ferns of Britain and Northern Europe. Harper Collins Publishers.
31. Gaston K.J. 2003. The Structure and Dynamics of Geographic Range, Oxford University Press.
32. Glandt D. 1991. The vegetation structure preferred by the sand lizard (Lacerta agilis) and the common lizard (Lacerta vivipara) in an experimental outdoor enclosure. *Acta Biol. Benrodis*, 3: 79-86.
33. Glandt D. 1995. Seasonal activity of the sand lizard (Lacerta agilis) and the common lizard (Lacerta vivipara) in an experimental outdoor enclosure. In: *Scientia Herpetologica*, (Llorente, G., Santos, X., Carretero, M.A.. (Eds)). Asociacion Herpetologica Espaniola, Madrid.
34. Gooddard P. & Spellerberg I. 1980. Reproduction as a factor in the conservation of Coronella austriaca Laur. In Southern England. *Bull. Ecol.* 11 (3/4): 138-143.
35. Gregory P.T. & Isaac L.A. 2004. Food habits of the grass snake in southeastern England: is Natrix natrix a generalist predator? *Journal of Herpetology* **38**: 88-95.
36. Greenberg C.H. 2001. Response of reptile and amphibian communities to canopy gaps created by wind disturbance in the Southern Appalachians. *Forest Ecology and Management*, 148: 135-144.

37. Grosse A. & Transehe N. 1929. List of the East Baltic Vertebrates. Komisijā pie J. Deubnera, Rīga [In Latvia]
38. Gruodis S. 1987. Amphibians and reptiles. In: *Ecological optimisation of agrolandscape,* (Sokolov, V.J. (Ed.)) Nauka Publishers, Moscow [In Russian with English summary].
39. Guisan A. & Hofer U. 2003. Predicting reptile distributions at the mesoscale: relation to climate and topography. *J. Biogeogr.* **30**: 1233-1243.
40. Heatwole H. 1977. Habitat selection in reptiles. In: *Biology of the Reptilia. Volume 7. Ecology and Behaviour A.* (Gans C., Tinkle D.W. (eds.)) Academic Press Inc., London.
41. House S.M. & Spellerberg I.F. 1983. Ecology and conservation of the sand lizard (Lacerta agilis) habitat in Southern England. *J. Appl. Ecol.* **20:** 417-437.
42. Fischer J. 1791. Versuch einer naturgeschichte von Livland. Koenigsberg.
43. Ingelog T., Andersson R. & Tjernberg M. (Eds.) (1993*). Red data book of the Baltic region. Part 1. Lists of threatened vascular plants and vertebrates.* Swedish Threatened Species Unit, Uppsala in co-operation with Institution of Biology, Riga.
44. IPCC. 2001. *Climate change 2001: the scientific basis. Contribution of working group I to the third assessment report of the Intergovernmental Panel on Climate Change.* Cambridge Univ. Press.
45. Jablokov A.V. (Ed.) 1976. *The Sand Lizard. Monographic description of the species.* Nauka Publishers, Moscow [In Russian].
46. Jędrzejewska B. & Jędrzejewski W. 1998. *Predation in vertebrate communities: the Białoweža Primeval Forest as a case study.* Springer-Verlag, Berlin, Heidelberg .
47. Kabucis I. (ed.) 2000. *Handbook of habitats. Protected habitats by European Union in Latvia.* Latvijas Dabas Fonds, Riga. [In Latvian].
48. Kavacs G. (Ed.) 1995. *The Encyclopaedia of Latvia's Nature. Vol. 2.* Latvijas Enciklopedija Publishers, Riga. [In Latvian]
49. Kavacs G. (Ed.) 1997. *The Encyclopaedia of Latvia's Nature. Vol. 4.* Preses nams Publishers, Riga. [In Latvian]
50. Kavacs G. (Ed.) 1998. *The Encyclopaedia of Latvia's Nature. Vol. 6.* Preses nams Publishers, Riga. [In Latvian]

51. Kosov S.V. 1983. The impact of some abiotic factors on daily and yearly activities of the grass snake. In: *Issues of experimental zoology,* Nauka I Tehnika Publishers, Moscow [In Russian]

52. Krebs C.J. 1989. *Ecological methodology.* Harper & Row Publishers, New York.

53. Kutt A. 1993. Initial observations on the effect of thinning eucalypt regrowth on heliothermic skinks in lowland forest, East Gippsland Victoria. – In: *Herpetology in Australia – a diverse discipline.* (Lunney, D., Ayers, D. (Eds.)). Royal Zoological Society of New South Wales.

54. Larsson A.M. 1995. Activity range and habitat selection by radio-tracked smooth snakes (Coronella austriaca) on the Swedish west coast. *Memoranda Soc. Fauna Flora Fennica,* 71: 103-105.

55. Lima A.P., Suarez F.J. & Higuchi N. (2001). The effects of selective logging on the lizards Kentropyx calcarata, Ameiva ameiva and Mabuya nigropunctata. *Amphibia-Reptilia* **22**: 209-216.

56. Lipsbergs J., Kačalova O., Ozols G., Rūce I., & Šulcs A. 1990. Popular Red Data Book of Latvia. Animals: Distribution, Ecology, Conservation. Zinātne, Rīga [In Latvian].

57. Ļuta K. 1973. The smooth snake in Mērsrags, Latvia. In: *Dabas un vēstures kalendārs 1974. gadam.* Zinātne, Rīga: 112. [In Latvian].

58. Madsen T. 1984. Movements, home range size and habitat use of radio-tracked grass snakes (Natrix natrix) in Southern Sweden. *Copeia* **1984**: 707-713.

59. McAlpine D.F. & Dilworth T.G. 1989. Microhabitat and prey size among three species of Rana (Anura: Ranidae) sympatric in eastern Canada. *Can. J. Zool.* 67: 2244-2252

60. Ognev A.V. & Laptikov J.M. 1989. Distribution and some ecological features in the adder, Vipera berus, in the Moscow District In: *Amphibians and reptiles of the Moscow Region*, (Janshin, (Ed.)) Nauka Publishers, Moscow [In Russian].

61. Pētersone A. & Birkmane K. 1980. *A guide to plants of the Latvian SSR, 2^{nd} edition.* Zvaigzne, Riga. [In Latvian]

62. Phelps T.E. 1978. Seasonal movement of the snakes Coronella austriaca, Vipera berus and Natrix natrix in Southern England. *British Journal of Herpetology* **5**: 755-761.

63. Pikulik M.M., Baharev V.D. & Kosov S.V. 1988. *Reptiles of Belarus*. Nauka i Tehnika Publishers, Minsk. [In Russian].

64. Prestt I. 1971. An ecological study of the viper Vipera berus in southern Britain. *J. Zool.* **164**: 373-418.

65. Priedītis N. 1999. *Latvian forest: nature and diversity.* WWF, Riga.

66. Pupiņš M. & Škute A. 1992. Herpetofauna of the Ilgas vicinity. *LDPAB DPI organizācijas IB* 2: 15-16 [In Latvian]

67. Raxworthy C.J., Martinez-Meyer E., Homing N., Nussbaum R.A., Schneider G.E., Ortega-Huerta M.A. & Peterson A.T. 2003. Predicting distributions of known and unknown reptile species in Madagascar. *Nature* **426**: 837-841.

68. Sartorius S.S., Vitt L.J. & Colli G.R. 1999. Use of naturally and anthropogenically disturbed habitats in Amazonian rainforest by the teiid lizard Ameiva ameiva. *Biological Conservation* **90**: 91-101.

69. Shine R. & Mason R.T. 2004. Patterns of mortality in a cold-climate population of garter snakes (Thamnophis sirtalis parientalis). *Biological Conservation* **120**: 205-214.

70. Siliņš J. & Lamsters V. 1934. *Reptiles and amphbians of Latvia.* Valters un Rapa, Riga [In Latvian]

71. Spellerberg I.F. 1986. Conservation of reptiles in Britain and their role in monitoring changes in biological systems. In: *Studies in Herpetology* (Roček Z. (ed.)) Charles University, Prague: 747-752

72. Spellerberg I.F. 1988. Ecology and managment of reptile populations in forests. *Quarterly Journal of Forestry*, **82**: 99-109.

73. Spellerberg I.F. & Phelps T.E. 1977. Biology, general ecology and behaviour of the snake, Coronella austriaca Laurenti. *Biol. J. Linn. Soc. London* **9** (2): 133-164.

74. Spuris Z., Lapiņa I. & Vīksne J. 1974. *Protected animals of the Latvian SSR.* Zinātne, Rīga [In Latvian]

75. Stanners D. & Bourdeau P. 1994. *Europes's Environment: The Dobris Assessment.* Office for official publications of the European communities, Luxembourg).

76. Strijbosch H. 1988. Habitat selection of Lacerta vivipara in a lowland environment. *Herpetological Journal* 1: 207-210.
77. Strijbosch H. 1999. Importance of rivers in shaping original Euro-Mediterranean lizard habitats. *Natura Croatica* 8 (3): 331-337.
78. Stumpel A.H.P. 1985. Biometrical and ecological data from a Netherlands population of Anguis fragilis (Reptilia, Sauria, Anguidae). *Amphibia-Reptilia* **6**: 181-194.
79. Stumpel A. H. 1988. Habitat selection and management of the sand lizard Lacerta agilis L., at the Utrechtse Heuverlug, Central Netherlands. *Mertensiella* **1:** 122-131.
80. Stumpel A.H.P. 1992. Reptile management problems in Netherlands heathlands. In: *Proceedings of the 6th Ordinary General Meeting of the Societas Europea Herpetologica. 19-23 August 1991 Budapest, Hungary*, (Korsos, Z., Kiss, I. (Eds.)) Hungarian Natural History Museum, Budapest.
81. Tabachnik B.G. & Fidell L.S. 1996. *Using multivariate statistics, 3rd edition.* Harper Collins College Publication, New York.
82. Temnikova N.S. 1958. *Climate of Latvian SSR.* Latvian SSR Academy of Sciences Publishers, Riga. [In Russian].
83. Toporkova L.J. 1973. Amphibians and reptiles of Ural. In: *Fauna of the European North, Ural and Western Siberia*, Uralian State University, Sverdlovsk.
84. Turlajs J. (Ed.) 1998. *Atlas of Latvian History.* Apgads Jana Seta Publishers, Riga. [In Latvian].
85. Viitanen P. 1967. Hibernation and seasonal movements of the viper, *Vipera berus berus* (L.), in Southern Finland. *Annales Zoologici Fennici* **4**: 472-546.
86. Voitehov M.J., Leshcheva T.S., Flint V.E., Formozov N.A & Garushjanc K.J. 1989. Short notes on amphibian and reptile fauna of the Moscow City and the Moscow District. In: *Amphibians and reptiles of the Moscow Region* (Janshin A. (Ed.)) Nauka Publishers, Moscow. [In Russian].
87. Walther G.-R., Post E., Convey P., Menzel A., Parmesan C., Beebee T.J.C., Fromentin J.-M., Hough-Guldberg O. & Bairlein, F. 2002. Ecological responses to recent climate change. *Nature* **416**: 389-395.
88. Zamolodchikov D.G. & Avilova K.V. 1989. Materials on biology of the common lizard, Lacerta vivipara, in a high moor in Western Moscow region.

In: *Amphibians and reptiles of the Moscow Region*. Nauka, Moscow. [In Russian]

89. Zirnis E. 1980. *Rare reptiles and amphibians of the Latvian SSR*. Bachelor's thesis. Latvian State University, Rīga [In Latvian].
90. Zuiderwijk A., Groenveld A. & Smit, G. 1998a. Monitoring of reptiles in the Netherlands. In: *Studies in herpetology* (Miaud, C., Guyetant, R. (Eds)), Societeas Herpetologica Europaea, Le Bourget du Lac.
91. Zuiderwijk A., de Wijer P. & Janssen I. 1998b. The decline of a grass snake metapopulation near Amsterdam. In: *Studies in herpetology* (Miaud C. & Guyetant R. (Eds.)) Societeas Herpetologica Europaea, Le Bourget du Lac.